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THE ANATOMY OF THE PELECYPOD FAMILY ARCIDAE

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ABSTRACT

The ancient and geologically important family Arcidae is estimated to comprise upwards of eleven hundred species and subspecies. The greater number of these are in a fossil state, and obviously have been classified on the basis of shell characters. The same is true of many living species, and where anatomical studies have been made they usually were limited to some definite organ or system. While such a procedure results in supplying the morphologist with important data, it may lead to faulty conclusions on the part of the systematist. In the present work, for example, there are two types of individuals with identical shells and declared to be of the same species, whereas their anatomy proves them to be distinct. Furthermore, there are subspecies where the shells are unlike, while the internal organization would scarcely warrant subspecific rank. And again there are genera where a definite organ or system is of distinct diagnostic value; in other genera it is of doubtful worth. Under such circumstances it is apparent that comparisons must rest upon the entire organization of each species rather than upon one or a few selected elements.

In the present study the anatomy of thirty-two species and subspecies has been described and figured in more or less detail. No attempt has been made to modify the existing scheme of classification beyond pointing out in the final paragraphs where certain changes appear to be in order. It may be added that the relatively wide range of differences between species of certain genera suggest further revisions, but the importance of these variations can be determined only after a study has been made of a greater number of additional species.

According to a recent review of the family Arcidae (Reinhart '35), it is conservatively estimated that not less than twelve hundred species are included in the group. The majority of these are fossil forms, and obviously have been classified on the basis of shell characters. The same is true of many recent species. On the other hand numerous investigators are responsible for detailed studies of the urogenital, circulatory or digestive systems or of various external features. Only a very few species have been studied from the standpoint of their entire organization.

During the course of the present investigation it became evident that a scheme of classification based upon shell characters alone may lead to erroneous conclusions. And, speaking generally, it was equally evident that comparisons based upon a single organ or system also may prove to be untrustworthy. In one subgenus or genus fundamental differences may appear; in other cases they may not.

In such a study the nervous system appears to be highly conservative, and little subject to change. The same apparently is true of the urogenital system. The circulatory system as a whole is unreliable, but where the pericardial cavity is single or double or divided by a dorsal or ventral septum the situation is important, especially when taken into considera-

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tion along with other features. The various types of abdominal sense organs frequently are of service in determining relationships, and the number and arrangement of the muscles bridging the visceral cavity may afford an important clue. The digestive system is highly plastic, and often there is a marked degree of variation even in the members of the same subgenus. Nevertheless the configuration of the stomach, the position of the bile ducts and the length of the intestine may be important factors in tracing the phylogeny of the group. In short, the most satisfactory classification must rest upon evidence supplied by the study of the entire organism as various authors have maintained.

Finally, it may be added, the present investigation is not presented as a critical scheme of classification, but rather as a contribution which it is hoped may prove to be of service to students who are confronted with the problem of tracing the phylogeny of this ancient and geologically important group. To this end the concluding paragraphs are devoted to a listing of the more important resemblances and differences between the different species.

Methods and Material

In the majority of species a definite technique was employed in the preparation of material for dissection as well as for the dissection process itself. In most instances the shape of the shell is such that the removal of the body usually results in a serious amount of damage to the softer tissues and organs. Accordingly the shell was removed by dissolving it in dilute nitric acid. Furthermore, in the majority of the species the visceral cavity, as usual, contains the gonad, digestive gland and the larger part of the digestive system, but unlike the majority of mollusks these organs are bound together with connective tissue of extreme tenacity. Even in those species where this condition is not so pronounced the digestive system is frequently of such delicacy that no satisfactory dissection of the ordinary type is possible without the consumption of an inordinate amount of time. Hence after repeated failures and partial successes each specimen was divided sagittally along the mid-line, and the dissected structures of each half were then combined in the final sketch. In some cases where the intestinal loops were of a more than usually complicated type the coils of each half were modelled in plastic clay and the two halves were then combined.

The various species figuring in the present study are listed in the appended table. *Arca imbricata* was identified as such by Dr. H. G. Schenck and Miss Myra Keen of the Department of Palaeontology, Stanford University. They also, together with Dr. P. W. Reinhart, are responsible for the identification of *Barbatia decussata*, and for *Scapharca* sp. collected off the coast of Senegal, Africa. The remaining species were classified in the National Museum.

Arca

Owing to various primitive features, this subgenus has been the subject of investigations on the part of numerous authors during the past hundred and fifty years. Much of this work has centered in the arrangement and structure of the circulatory system and its possible origin. The structure of the gills likewise has received considerable attention, and Matthias ('14) has made an exhaustive study of the digestive system and the circulation to a less extent.

In the present collection this subgenus is represented by six typical species, *bouvieri*, *imbricata*, *noae*, *pacifica*, *umbonata* and *zebra*. From the standpoint of external appearance all of these species exhibit a fairly close resemblance to each other (compare the figures of the first four and last plates). The palps are more or less vertical in position, the byssus cavity is well developed, and the abdominal sense organs are related to the anal opening in essentially the same fashion throughout. There is considerable variation with respect to the pedal retractors correlated possibly with the nature of the environment. They are relatively small in *A. pacifica*, of about average size in *A. bouvieri*, *imbricata* and *umbonata* and large in *A. zebra*.

The digestive system varies to a considerable degree, and yet there are certain general features common to all. The mouth holds a position adjacent to the lower border of the

TABLE I

Species	Locality
Arca bouvieri Fischer	Off Senegal, Africa
Arca imbricata Bruguiere	Fiji Ids.
Arca sp.	Fiji Ids.
Arca noae Linné	So. of Triest, Italy
Arca pacifica Sowerby	Gulf of California
Arca umbonata Lamarck	Porto Rico
Arca zebra Linné	Porto Rico and Florida
Barbatia barbata Linné	Florida
Barbatia decussata Sowerby	Off Sierra Leone, Africa
Barbatia (Cucullaearca) candida Gmelin	Key West
Barbatia (Acar) gradata Broderip & Sowerby	Gulf of California
Barbatia (Acar) pernoides Carpenter	Off L. California
Barbatia (Acar) reticulata Gmelin	Virgin Ids.
Arcopsis adamsi Smith	Florida
Arcopsis solida Broderip	Gulf of L. California
Bathyarca pectunculoides Scacchi	So. of Halifax
Trisodos tortuosa Linné	Philippine Ids.
Anadara bisenensis Schenck & Reinhart	Inland Sea, Japan
Anadara granosa Linné	China
Anadara (Scapharca) concinna Sowerby	Gulf of California
Anadara (Scapharca) auriculata Lamarck	Florida
Anadara (Scapharca) transversa Say	Long Island Sound
Anadara (Scapharca) sp.	Off Senegal, Africa
Anadara (Cunearca) chemnitzi Philippi	Porto Rico
Anadara (Cunearca) incongrua Say	Off So. Carolina
Anadara (Cunearca) perlabiata Grant & Gale	Off Peru
Argina pexata Say	Long Island Sound
Noetia ponderosa Say	Florida
Cucullaea granulosa Jones	Suruga Gulf, Japan
Glycymeris americana DeFranco	Porto Rico
Glycymeris longior Sowerby	Off Argentine, S. Am.
Glycymeris migueliana Dall	Off So. California
Glycymeris pectiniformis Linné	Philippine Ids.
Glycymeris subobsoleta Carpenter	Off Oregon, U.S.A.

anterior shell adductor, and its relation to the palps follows the usual plan. The esophagus is comparatively short in *A. bouvieri* and *A. zebra*, of average length in *A. umbonata* and comparatively long in *A. noae*, judging from the single specimen in hand. In every case there is a dorso-ventral compression. Owing to the large size of all of the specimens, no sections were made, and the presence or absence of longitudinal grooves and ridges or of glandular elements was not determined.

Considerable attention was paid to any clearly marked indications of a special pharyngeal cavity or of a clearly defined section of the digestive tract between the mouth opening and a definite esophagus, but such appears to be absent not only in *Arca s.s.*, but in all of the other species treated in the present work. In several instances there were dilations in this region in the case of some of the specimens, whereas in other individuals of the same species these were absent. In *A. zebra* (Pl. III, Fig. 2) there was a marked enlargement of the esophagus, adjacent to the stomach, which was filled with crystalline stile secretion or material secreted by the esophageal glands. In *A. bouvieri* (Pl. IV, Fig. 2) the entire esophagus was distended with a mixture of some secretion and detrital material. In other individuals this section of the digestive tract was of even caliber throughout. It would be interesting indeed to ally the pelecypods in this respect with the gastropods, for example, but so far as present evidence is concerned it is negative.

The stomach presents such a wide range of variation that a detailed description is out of the question. A comparison of the figures on plates II, III, IV and XXII must suffice. From these it will be seen that macroscopically there is a fairly distinct line of demarcation between the esophagus and stomach. Furthermore, this last named organ comprises the well known divisions—the dorsal stomach proper, and a clearly defined ventral section or Magendarm of List ('02). In *A. umbonata* this dorsal region finds its most simple expression; in *A. zebra* it becomes more complex, becoming still more complicated in *A. bouvieri* and *A. noae*.

In this connection it should be noted that with respect to the stomach a certain amount of variation often occurs among individuals of the same species. In some instances this is due to distension as a result of large amounts of detrital material or crystalline stile secretion. The most extreme case of this type is represented on Pl. III, Figs. 2, 3. Both specimens were identified as *A. zebra*, and in each figure the right half of the stomach is shown, a portion of the left wall being reflected in Fig. 3. It will be noted that in Fig. 2 (from North Carolina) the posterior extremity of the stomach (pars pylorica of Matthias) is produced into a comparatively slender diverticulum, whereas in Fig. 3 (from Porto Rico) this region is much more voluminous. Also the course of the intestine is different in the two cases. It is possible that here we are dealing with distinct species, and not with a variation much wider than others discovered in the course of this work.

The ventral section of the stomach resembles that of *A. platei* and *A.* (*Barbatia*) *barbata*, as described by Matthias, where two prominent ridges, separated by a deep groove, are developed from the gastric epithelium. According to this same author, the groove serves to transfer the digested material into the intestine, while the larger channel, with which the smaller one communicates, secretes the crystalline stile.

In a few of the drawings the position of some of the ducts from the digestive gland (hepatopancreas) are indicated, but it is very probable that they represent a fraction only of those present. Matthias, for example, notes that there are 10 openings in *A. platei*, 11

in *A. noae* and 10 in *A. angulata*. The count is based upon the fact that the basal section of each duct is a non-glandular continuation of the gastric epithelium, which more distally unites with the follicles of the liver. This demands the use of sectioned material which in the present instance was utilized only in the case of various small species described in succeeding sections.

In all of the species the ventral section of the stomach is directed in an antero-ventral direction to a point adjacent to the pedal ganglia. From here the intestine, in a sweeping curve, extends posteriorly, and on the right side of the stomach makes its way beneath the heart to open on the ventral face of the posterior shell adductor. An exception to this rule occurs in *A. imbricata* where the intestine, upon leaving the stomach, extends posteriorly beyond the forward border of the pedal retractor before rising to the dorsal surface of the body (Pl. XXII, Fig. 1).

In *A. pacifica* (Pl. III, Fig. 7) and *A. bouvieri* (Pl. III, Fig. 6) the posterior margin of the anal opening has developed a small median flap which becomes a more prominent feature in some other species, notably *A.* (*Barbatia*) *barbata* (Pl. V, Fig. 10). Whether it serves as a sense organ or as a valve to close the anal opening remains another of many unsolved problems.

Thanks to the investigations on the part of several authors, we possess a clear picture of the circulatory system in several species of *Arca* and their allies. Accordingly in the present study a superficial examination only has been carried out. In every species there is wide degree of separation of the pericardial cavities and the contained auricles and ventricles; and in most instances a single anterior aorta courses along the dorsal surface of the body to the right of the mid-line (as in Pl. II, Fig. 8).

In the larger number of species treated in the present work an effort has been made to study and illustrate the various transverse muscles spanning the visceral cavity. But in the species of *Arca* we are considering here these structures are surprisingly small, and so delicate that, in the process of removing the gonad and digestive system, practically all of the muscle bundles were dislodged. Maceration methods were unsatisfactory, and further attempts accordingly were abandoned.

No study was made of the details of the urogenital system and, it may be added, that during the course of dissection considerable attention was paid to the nervous system, which closely resembles that of *Arca* sp. described in the next section.

Arca Sp.

The collection kindly supplied by Doctor van Straelen of the Brussels Museum included a single specimen with an attached label stating that it was collected in the Fiji Ids. on a reef. The shell was examined by Doctor Schenck who identified it as *Arca imbricata*. Subsequent dissection, however, revealed numerous features which indicated that if indeed this individual was a normal one it certainly should not be included in that genus. Upon request Doctor van Straelen supplied a second specimen from the same locality, which he had identified as *Arca imbricata*, a verdict with which Doctor Schenck agreed. Its anatomy showed it to be a typical *Arca*, and *imbricata* doubtless is the correct specific name. Until a further investigation is made this unique individual will be designated in the text and explanation of plates as *Arca* sp.

The chief external features of this species are illustrated on Pl. I. From these figures it will be seen that the palps of small, probably contracted, size are almost vertical in position, the gills are horizontal, and the byssus cavity is of large dimensions. This last named structure possesses a fairly flat roof with low ridges radiating from a sub-central position (Fig. 3). Originally it contained a hornlike highly compact secretion composed of a series of many concentric layers. In keeping with the high degree of development of this gland, the pedal retractors are of great size (Figs. 1, 7).

The abdominal sense organs are shown on Pl. II, Fig. 4. In a very broad fashion they resemble those of members of the preceding section (Pl. III, Figs. 6, 7, 9), and they very well may have evolved from a common type.

The mouth, holding the usual position (Pl. I, Figs. 2, 7), is a slitlike opening, and the esophagus throughout its entire extent is dorso-ventrally compressed. On Pl. II, Fig. 1, a portion of the esophageal wall and the anterior end of the stomach are reflected, giving the appearance of a prominent longitudinal ridge, but in reality, while ridges are present, they are of small size and extend from the mouth to the stomach.

The stomach itself is fairly accurately represented on Pl. II, Figs. 1, 2; hence a detailed description appears to be unnecessary. It may be added that the opening into the lower division of the stomach (Magendarm) is far to the right side adjacent to the great fold developed in the ventral wall of the upper gastric division.

Two bile duct openings are represented, and in addition there are several other very delicate depressions in the same general region that may represent additional openings.

In this particular individual the ventral section of the stomach was filled with crystalline stile material that had become almost as hard as stone in the alcohol preservative. Attempts to remove it were unavailing, and accordingly all that can be said is that this portion of the digestive tract possessed the usual form. The intestine also followed the same course as in the various species described above, coursing ventral to the heart and opening beneath the posterior shell adductor.

For an animal of this size (84 mm long) the visceral cavity is small, and it may be added that the transverse muscles are correspondingly slender and delicate. As in the case of *Arca* s. s., dissection methods played havoc, and all attempts to determine their distribution were abandoned.

Regarding the circulatory system, certain features appear to be definitely established. As may be seen on Pl. I, Fig. 1, the ventricles are widely separated, and in this respect they resemble *Arca* s. s. The vessels with which they connect, however, are unique. By injecting air into these their course was followed without great difficulty, and so far as the present specimen is concerned their position is believed to be accurately represented in the figure. As in other species, the two ventricles are united across the mid-line, but in their course two branches are developed which follow a route toward the anterior end of the animal. The one to the right of the mid-line, the larger of the two, probably corresponds to the anterior aorta of *A. bouvieri* (Pl. II, Fig. 8), for example. Its mate, on the other side of the mid-line, was traced as far forward as the pedal protractor where it branched and became lost to view. The main aorta, upon reaching the retractor, bent downward, gave off a small branch to the region adjacent to the cerebral ganglia, and then pursued a fairly direct course through the visceral cavity, giving off branches by the way, to become lost between the halves of the pedal retractor. More unusual is the fact that this same

transverse vessel uniting the ventricles also gave rise to a median vessel, the posterior aorta, which was followed to a point where it passed beneath the intestine.

In the majority of the species in this family the mantle presents a more or less clouded appearance due to a glandular development comparable to that existing in many nuculids (Heath '37). In *A. imbricata*, on the other hand, the mantle is crystal clear, and but little dissection is needed to lay bare the main features of the nervous system.

Upon removing the anterior shell adductor the supra-esophageal ganglia are seen to be ellipsoid in form, and, where ganglion cells exist in noticeable quantity, are of a slightly yellowish tinge. These ganglia are prolonged into the usual pedal and visceral connectives are represented in Pl. I, Fig. 6. At the union of each cerebral ganglion and its commissure a strong nerve (*m*) is developed which supplies the mantle and the shell adductor. All of these branches subdivide and form a plexus which probably extends over the entire mantle. In this particular individual the strongest nerves from the supra-esophageal ganglia extend along the mantle border, and become continuous with the main branches from the visceral ganglia. A small nerve arises from the ventral face of each cerebral ganglion, and passes into the dense tissue surrounding the mouth. It appears, though this is not certain, that these two branches are destined to enter the palps.

The visceral ganglia, attached to the ventral surface of the posterior shell adductor, are conical in form and originate five pairs of nerves (Pl. II, Fig. 3). The median pair (*g*) extends into the tissue which supports the free tip of the gills, and although no sections were made it is probable that they innervate the osphradia. The next most median pair (*s*) extends into the region of the rectum and evidently innervates the abdominal sense organs shown in Pl. II, Fig. 4. The remaining pairs are distributed to the mantle, the exception being a delicate pair (*b*) which have been traced as far forward as the heart, and, with the exception of a small division extending into the mantle, are confined to the body wall between the mantle and the mid-line of the body.

In all of the other species described in this paper the gonad comprises a system of relatively stubby follicular outgrowths essentially the same as those of *Arca noae* (Pl. II, Fig. 5). On the other hand in this species the follicles, if such they prove to be, are extremely elongated, presenting the appearance of a tangled mass of nematode worms (Pl. II, Fig. 6). Unfortunately it was not possible to keep this system intact while carrying on the customary process of dissection. Hence the connection of the "follicles" or threads with the main duct was not determined, much less the relation of the gonoduct and kidney.

Some of the tubes, undisturbed in the process of dissection, were sectioned, and, although the material was not especially favorable for a careful histological examination, the following facts appear to be well established. Certain it is that these so-called threads or follicles are composed of a single layer of polygonal cells with central nuclei. And it is equally true that these same threads are canals containing smaller tubes of two sizes. Furthermore, appearances indicate that this individual was a male, and that spermatocytes are developed in the larger of these enclosed tubules (Pl. I, Fig. 8), and are transported through the smaller canals. However, there is no actual proof that such is the case since no sperms were present. Obviously there are wide gaps in this description, and it is hoped that these may be filled by other investigators.

Barbatia

The two typical species of this subgenus are *B. barbata* and *B. decussata*. The first of these and last have been the objects of investigation on the part of several authors, notably Pelseneer, Theiler and Matthias. For the sake of comparison, and owing to a somewhat different viewpoint together with various additional facts, a more or less cursory description follows.

Externally these species agree fairly closely in their appearance Pl. V, Figs. 1, 2). The mantle exhibits a slight glandular development, its appearance in *B. barbata* being represented on Pl. XX, Fig. 2. The byssus cavity is well developed, and the abdominal sense organs are similar in *B. barbata* (Pl. V, Fig. 10) and *B.* (*Cucullaearca*) *candida*. Owing to the state of preservation of *B. decussata* their exact form could not be determined.

The digestive system of *B. barbata* has been the subject of a comprehensive study on the part of Matthias. His figures correspond fairly closely to Figs. 6, 12 on Pl. XV. One marked difference exists in the present case with respect to the ventral division of the stomach. Evidently in a normal state two prominent ridges in the lining epithelium form two troughs, the larger containing the crystalline stile, and a smaller one permitting the passage of nutritive material. In the two specimens of the present collection the crystalline stile secretion was extremely hard, and evidently abnormally swollen to such an extent that it had flattened the ridges completely.

The internal features of the stomach of *B. barbata* show it to be unusually simple with dilations and ridges reduced to a minimum (Pl. XV, Figs. 6, 12). In *B. decussata* the state of preservation was far from being ideal, and in addition the gastric epithelium was dislodged to a large extent with the removal of the crystalline stile. So, while finer details probably are lacking, it is believed that the figures (Pl. IV, Fig. 9, Pl. V, Fig. 3) represent the main characteristics, which, it may be added, are more complex than in the foregoing species.

The intestine is similar to that of typical arcids, *A. noae* being a good example. As other investigators have observed, the gut passes beneath the pericardial cavity.

The circulatory system of *B. barbata* has been investigated by Ménégaux and by the authors noted above. According to Matthias, two separate pericardial cavities exist. From the figure of *B. decussata* by Pelseneer ('11, Pl. II, Fig. 10) it is clear that but one is present in that species.

The chief transverse muscles of the visceral cavity are shown on Pls. V, XVII.

Evidently no study has been made of the nervous and urogenital systems by other authors, and this state of affairs continues since none of the species in the present collection was sectioned.

Acar

This subgenus includes three species, *A. gradata*, *A. reticulata* and *A. pernoides*. The chief external features are represented on Pl. VI, Fig. 1, and Pl. XIV, Fig. 2. On the first plate the figure of *A. gradata* shows a sharp fold in the external gill plate, but this was found to be lacking in other specimens. There is a glandular development of the external epithelial layer of the mantle, scattered gland cells staining darkly with Delafield's haematoxylin being a conspicuous feature in *A. reticulata*. The abdominal sense organs of *A. pernoides* are shown on Pl. V, Fig. 9. Those of *A. gradata* are similar. The byssus is a prominent structure with its main features shown on Pl. XII, Fig. 11.

A reconstruction of the digestive system was made by means of sections for each of the three species, and the results show that all are constructed upon the same general relatively simple plan. In *A. gradata* the esophagus is dorsoventrally compressed; in the others it is circular in cross section.

In three specimens of *A. pernoides*, preserved in Bouin's solution and stained in Delafield's haematoxylin, there are peculiar outgrowths of the esophageal wall. These comprise three pairs. The first one is situated in the region of the cerebral ganglia (Pl. XXII, Fig. 6). The other two are closely associated, and are much closer to the stomach. At first the appearance of these structures suggested that they were ducts communicating with some of the liver follicles in the immediate neighborhood. A closer examination, however, clearly indicated that they end in stubby outgrowths of a unique character. Some of the cell elements contain an abundant supply of a darkly staining secretion, and it may be assumed that they have the same function as similar though more slender cells characteristic of the esophagus in general. The unique feature concerns several large cells which form wartlike projections from the external surface of the duct (Pl. XXII, Fig. 8). These contain a finely granular secretion which stains but lightly. At the present time it is futile to attempt to homologize these structures with the glands of other mollusks. Provisionally they may be termed esophageal glands since their position scarcely warrants the assumption that they are of buccal or pharyngeal origin.

The bile ducts in *A. reticulata* number not less than thirteen. Two open on the right side of the stomach, two are on the left face, while the others are distributed over the ventral surface (Pl. VI, Fig. 9). In *A. gradata* (Pl. XXII, Fig. 7) two bile ducts connect with the anterior face of the stomach, the much larger one on the right side extending beyond the mid-line and ventrally as far as the junction of the stomach and intestine. Another duct on the left side is situated slightly dorsal to the first pair, and yet another enters the right side. In *A. pernoides* there are three main ducts, one attached to the ventral gastric wall, another dorsal to it, and another farther back on the right side (Pl. XXII, Fig. 6).

The course of the intestine is much the same as in *Arca* s. s., and as in that subgenus the heart is in a dorsal position.

A reconstruction of the heart was made in the case of *A. reticulata* (Pl. VII, Fig. 8). Ventral to the heart the pericardial cavity is continuous; dorsally it is divided by a delicate septum. Auriculo-ventricular valves are present. A very general sketch of the heart of *A. gradata* is shown on Pl. XIII, Fig. 9; of *A. pernoides* on Pl. VI, Fig. 6. In this first named species the pericardium is continuous both above and below the heart, whereas in *pernoides* there are two distinct cavities.

The urogenital system was reconstructed in the case of *A. pernoides* (Pl. VI, Fig. 8) and of *A. reticulata* (Pl. XV, Fig. 9). In both of these species the relation of the various elements is essentially the same. A comparatively short canal from the kidney unites with the gonoduct close to the external opening, while the renopericardial funnel enters the kidney a short distance away. This state of affairs is practically the same as that described by Odhner ('12) for *Arca glacialis*.

The gonad is typical in its position and its relation to the kidney. In *A. reticulata* the reproductive follicles were empty, and their epithelial lining was undeveloped, indicating that the reproductive season was over. The gonad of *A. gradata* contained a large number of ova in various stages of development. Two specimens of *A. pernoides*

were males; the third was packed with developing sperms and ova which appeared to be fully matured (Pl. XXII, Figs. 9, 10). Whether or not this is a case of progressive hermaphroditism or proterandry must await an answer until an examination is made of individuals collected at different seasons and of various sizes.

The nervous system was reconstructed from sections in the case of *A. reticulata* (Pl. VI, Figs. 4, 5) and *A. pernoides* (Pl. XXII, Fig. 5). In the first named species the brain is typical of other members of the family; in the second it is distinctly bilobed. It will be recalled that Stempell ('93) and Pelseneer ('11) emphasized the fact that a bilobed brain exists in the protobranchs, and the two divisions were believed to represent cerebral and pleural ganglia. This indeed may be the true interpretation, although the origin and distribution of the related nerves casts some doubt upon their exact homologies (see Heath '37).

In *A. pernoides*, on the other hand, the picture appears with greater distinctness. The ventral lobes, corresponding to the cerebral ganglia in gastropods, for example, are united as usual by a commissure, and connectives lead off to the visceral ganglia. Distinct connectives also join them with the dorsal components, each of which supplies a heavy nerve to the mantle and a connective to the pedal ganglion. In other words the dorsal division resembles the pleural ganglion in many other mollusks. The cerebro-pedal connective may indeed be lacking or it may be represented by fibers which are associated with the pleuro-pedal connective.

Otocysts in the Arcidae are seemingly of rare occurrence. Pelseneer ('11), evidently citing the work of Carazzi ('02), states that they may occur in *Arca*. I can find no other references in the literature. They certainly are present in the three species of *Acar* in this collection. In the only sectioned specimen of *A. reticulata* they are attached to the muscles of the body wall opposite to the pedal ganglia. In *A. pernoides* also they are in contact with the body wall, and may be opposite to the pedal ganglia or considerably behind them. In the only sectioned specimen of *A. gradata* a slender muscle band spans the body cavity posterior to the pedal ganglia, and each otocyst is imbedded in this band about halfway between the outer body wall and the mid-ventral line of the body.

In a review of the genus or subgenus *Acar* by Reinhart ('39), several species are considered, among them the three represented in the present collection. From this account it appears that, on the basis of shell characters, some authors have considered *A. reticulata* and *A. gradata* to be conspecific. Reinhart, on the other hand, calls attention to slight differences in the hinges which are "probably of specific or at least subspecific importance," and this verdict certainly is correct when the internal anatomy is taken into consideration. In *A. gradata* the pericardial cavity is continuous both above and below the intestine, there are four main bile ducts, and the otocysts are situated at a considerable distance from the body wall, to mention only a few details. In *A. reticulata* a septum separates the pericardium dorsal to the gut, there are not less than thirteen bile ducts, and the otocysts are attached to the body wall.

Strong ('32) has shown that *A. bailyi* is a synonym of *A. pernoides*, and although there is a close resemblance to *A. gradata*, when the shells are compared, this same author considers them to be distinct. Reinhart agrees with this conclusion, calling attention to the fact that "although *gradata* and *pernoides* appear closely related, *pernoides* differs in being considerably smaller and having a different distribution than *gradata*. For these reasons,

pernoides should be considered distinct from *gradata*, as Strong concluded." From the standpoint of the internal anatomy this is indeed a legitimate conclusion. *Acar pernoides* is distinctly different from any other species in the present collection.

Cucullaearca

This subgenus is represented by a single species, *C. candida*. Externally it bears a fairly close resemblance to *B. barbata*. The mantle lacks any visible glandular development in the single available individual. The byssus is constructed upon much the same plan as in *B. decussata* (Pl. IV, Fig. 12). The region adjacent to the abdominal sense organs is heavily pigmented, but it is evident, nevertheless, that these sensory structures conform to the pattern of those in *B. barbata*.

The digestive system (Pl. V, Figs. 4, 5) is somewhat more complicated in this species than in *B. barbata*, for example but the difference between the two is no wider than is known to occur between species of other subgenera.

There is a general resemblance between the muscles of the visceral cavity in this species and those of *B. barbata;* it is more remote when compared to those of *B. decussata* (Pls. V, VII, XVII).

In the figure representing the general appearance of this species from the dorsal side, the shape of the heart and the origin of the dorsal aorta are shown (Pl. IV, Fig. 7). In this particular specimen the ventricles or ventricular pouches were gorged with coagulated blood, which may account for the fact that dye injected on one side of the mid-line, failed to cross over to the other side. Sections are needed to determine if the pericardium is single or double.

Various authors have noted that there is a distinct relationship between this subgenus and typical *Barbatia* species. Nevertheless there evidently are distinct differences, at least insofar as shell characters are considered, for Reinhart ('35) writes that "*Cucullaearca* comprises a clearly recognizable group." Hence some of the differences noted above may be of diagnostic value. More extensive and intensive study is needed before this point can be settled.

Arcopsis

This subgenus is represented by two species *A. adamsi* and *A. solida*. In both of these the entire mantle presents an opaque appearance due to a glandular development of the external epithelial layer such as is known to occur in the Nuculidae (Heath '37). Sections stained with Delafield's haematoxylin were made, and while the material is not favorable for a detailed study it is certain that the component cells are slender elements with nuclei adjacent to the external surface (Pl. VIII, Fig. 13). The remainder of each cell contains finely granular secretion unaffected by the dye.

The arrangement of the palps and gills in *A. solida* are shown on Pl. VII, Fig. 10. From a reconstruction of sections of *A. adamsi* it develops that the anterior portion of the foot is traversed by a shallow longitudinal furrow which more posteriorly communicates with a fairly deep cavity characterized by a median longitudinal fold bordered by a few others of smaller size (Pl. VIII, Fig. 9). Also, from the study of sections, it appears that in *A. solida* the same general plan exists, the chief difference being in the relatively greater development of the glands. In both species a definite byssus secretion is present. In

three specimens of *A. solida* the abdominal sense organs were unusually indistinct, the clearest being the one shown on Pl. VII, Fig. 4. Owing to the small size of *A. adamsi* (approximately 7 mm in length) these organs were even more indistinct, but there are some evidences that they resemble those of *A. solida*.

The digestive system is essentially the same in both species. As may be seen in the drawing of the longitudinal section (Pl. VII, Fig. 2) the, esophagus is devoid of any noteworthy features. In two sectioned individuals of *A. adamsi* this organ is almost circular in cross section. In *A. solida* it is exceptionally slender, relatively thick walled and is elliptical in outline. Without any clearly marked line of separation it unites with the stomach. This last named organ, represented on Pl. VIII, Fig. 8, is likewise a simple structure with heavy folds in the ventral section as its most prominent feature.

The position of the bile ducts is shown in a reconstruction of the digestive system of *A. adamsi* (Pl. VIII, Fig. 2). There it may be seen that the anterior end of the stomach projects forward beyond its union with the esophagus, and into this pouch two unusually elongated ducts enter from the digestive gland. The appearance of these ducts in cross section is shown on Pl. VII, Fig. 3. In a position more posterior and nearer the dorsal surface of the stomach a second pair of ducts have their origin. These in section are represented on Pl. VIII, Fig. 14. In *A. solida* the number and situation of these ducts are essentially the same.

In *A. adamsi* the heart appears with exceptional clearness, and accordingly a reconstruction was made of this portion of the circulatory system. From Pl. VIII, Fig. 1, it will be seen that the pericardium is a single cavity, and, as shown in Fig. 6 of this same plate, the ventricular pouches are united dorsal to the intestine by a spacious transverse channel which anteriorly gives rise to the dorsal aorta. In ventral view (Pl. XV, Fig. 2) the vessels, which connect with the ventricles and originate the ventral aorta, are comparatively slender, and their cavities are somewhat ill-defined.

In the only sectioned specimen of *A. solida* the pericardium is a single cavity, the ventral aorta and its connections are clearly defined, but the dorsal union of the ventricular pouches is very difficult to trace. Even in gross dissection this holds true. In one individual only was it possible to trace the dorsal union of the heart, and even there it was tenuous indeed. Auriculo-ventricular valves are present.

As to the muscular system, the adductors are well developed, and the pedal musculature is at least of average size. On the other hand, the muscles spanning the visceral cavity are exceptionally weak. Sections of *A. adamsi* show a few strands in the neighborhood of the mouth, and not more than four or five elsewhere in the cavity. In *A. solida* they appear to be somewhat more numerous, but their exact number and distribution remain uncertain owing to the fact that in tracing the digestive system they were dislodged to a great extent.

The main features of the nervous system are essentially the same as in *B. (Acar) reticulata.*

The urogenital system of *A. solida* is a close counterpart of this organ in *Trisodos tortuosa.* The main outline of the entire system was not determined, but the union of the terminal section of the gonoduct with the kidney proper and with the renopericardial canal is the same, the only marked difference being the somewhat longer and more tortuous course of the renopericardial canal.

Bathyarca

This genus is represented by one species, *B. pectunculoides*, with an average length of 10 mm.; accordingly the greater portion of the following description is based upon sections and reconstructions.

The external appearance of the body is represented on Pl. IX, Fig. 6. From this it will be noted that the palps are comparatively short, and the ill-defined grooves are confined to the more dorsal portions of these organs (Pl. VIII, Fig. 4). From sections it also is evident that the greater portion of the mantle is glandular, the cells closely resembling homologous elements in *Arcopsis adamsi* (Pl. VIII, Fig. 13).

Pelseneer ('11) in his account of the anatomy of *Bathyarca sinuata* describes and figures two peculiar folds of the mantle in the posterior end of the body. Similar organs exist in the present species (Pl. VIII, Fig. 15). Regarding their function, Pelseneer describes them as "une sort de tube inhalant dont les deux moitiés ne sont pas soudées." This appears to be a reasonable assumption, although the term exhalent may be a more accurate term.

In support of the view that these folds may function as a siphon it is to be noted that they are well supplied with muscles (Pl. VIII, Fig. 5), and it may well be that on occasion they may take the position indicated by the dotted lines in Pl. IX, Fig. 4, and so form a siphonal chamber.

Immediately above the attachment of each scoop just described the epithelium lining the inner face of the mantle is developed into a clearly defined circular disc (Pl. VIII, Fig. 5, *d*). While the preservation is not the best, the component cells appear to be of two main types, goblet cells of various sizes and interstitial or supporting cells. The larger goblet cells contain a yellowish secretion after treatment with Delafield's haematoxylin. No reasonable suggestion of their possible function comes to mind.

The byssus system comprises, first, a narrow furrow with delicately corrugated walls that extends along the anterior half of the foot. Posteriorly this groove leads into a deep depression containing a high median fold. The anterior half of this fold is non-glandular; the posterior half, on the other hand, is richly supplied with gland cells that evidently form the byssus (Pl. VIII, Figs. 7, 10).

As indicated on Pl. VIII, Fig. 11, and Pl. IX, Fig. 2, the esophagus is a simple tubular structure without any marked dilations or folds. As to its glandular activity conditions vary. In one specimen a very few cells only contain a secretion. In another individual a large number of cells (Pl. IX, Fig. 1) contain a darkly staining substance after treatment with Delafield's haematoxylin, which closely resembles the chromatin of an ordinary resting cell. This variation may be correlated with the feeding intervals, since the stomach of the first named specimen contained an abundance of detrital and nutritive material, while that of the second individual is nearly empty. In the more glandular specimen the distribution of the gland cells extends from the mouth to the stomach. No special aggregation at any point indicates a pharyngeal region.

The muscular coat of the esophagus is comparatively weak, consisting of delicate longitudinal fibers, and slender bundles of circular muscles, while the region about the mouth opening is slightly heavier due to radiating fibers which from their arrangement probably act as dilators.

No especial attempt was made to reconstruct the internal features of the stomach, and its general shape only is indicated (Pl. VIII, Fig. 11). The exact arrangement of the bile ducts likewise is somewhat diagrammatic, but the number and general position of these is fairly accurate (Pl. VIII, Figs. 3, 11). A gastric shield is present. The intestine follows essentially the same course as in *Arca* (Pl. VIII, Fig. 8), and passing ventrally to the pericardium it opens at the end of a slender stalk hanging freely in the mantle cavity (Pl. IX, Figs. 2, 6).

A reconstruction of the heart shows that it closely resembles that of *Barbatia barbata* as described by Ménégaux ('90). It also is similar to that of *Barbatia* (*Acar*) *reticulata* (Pl. VII, Fig. 8).

A reconstruction of the nervous system also indicates that it is built upon essentially the same plan as that of *Barbatia* (*Acar*) *reticulata* (Pl. VI, Figs. 4, 5).

The general configuration of the urogenital system closely follows that described by Odhner ('12) for *Arca glacialis*, and of *Barbatia* (*Acar*) *reticulata* in the present work (Pl. XV, Fig. 9). The gonoduct terminates in what may be termed an atrium, which, on the other hand, communicates directly with the kidney. The reno-pericardial canal also appears to connect with a diverticulum of the kidney, but its exact relations are uncertain.

Trisodos

This genus is represented by a single species, *T. tortuosa*. In certain general respects it resembles a typical *Arca*, yet at the same time it presents certain other features which are unique so far as the present collection is concerned. Of these unusual characters the most striking is its asymmetry. *Scapharca*, as is well known, possesses a shell in which a slight difference exists in the size of the valves of the shell, but in *Trisodos* this inequality is carried out to a high degree. Furthermore, these two types also differ in that the asymmetry of *Trisodos* does not affect the entire shell, but it occurs in the region posterior to the umbones, that is from a point slightly anterior to the heart (Pl. X, Fig. 13).

The palps are more inclined than in *Arca*, their posterior extremities being located nearer the mid-region of the body. Sections also indicate (Pl. X, Fig. 5) that the customary palp ridges of other species are here thrown into a series of minor folds. Another unique feature relates to the abdominal sense organs (Pl. XI, Fig. 1). In three specimens examined on this point the asymmetry in the posterior regions of the body has included these structures, the one on the right side being markedly larger than that on the left.

The byssus cavity (Pl. XI, Fig. 5) is well developed, but in no specimen was there a trace of a secretion although gland cells were much in evidence. The anterior fourth of the foot is traversed by a shallow longitudinal groove which more posteriorly is continued into the main larger and deeper depression. The lateral walls of the posterior half of this last mentioned section are dorsally fashioned into a series of delicate folds which disappear more ventrally, their place being taken by a band of gland cells. In the posterior half of the cavity the ridges of the walls are more pronounced, and at the extreme posterior end of the cavity they form a marked cluster reminiscent of the state of affairs in *A.* (*Barbatia*) *decussata*, for example.

In this species the digestive system is excessively delicate, and the connective tissue binding together the various organs of the visceral cavity is so highly tough and resistant that ordinary methods of dissection were fruitless. Accordingly the anterior half of the

body was sectioned, and the following description is based in large measure upon the reconstruction of sections.

The mouth in surface view exists as an elongated transverse slit, resembling *Arca* sp. (Pl. I, Fig. 2) in its shape and relation to the palps. From sections it may be seen that there is a fairly sharp line of demarcation between the smooth epithelium of the palps and the grooved walls of the esophageal tube (Pl. 10, Fig. 3). In a more or less irregular fashion these grooves and ridges extend to the stomach without any other marked peculiarities, and it may be added that throughout its entire extent the esophagus is dorsoventrally compressed.

Certain authors have noted that in a few species of arcids the esophagus shades gradually into the stomach, and in the present case it is difficult to determine the limits of the two. On Pl. X, Fig. 1, it will be seen that at a point approximately halfway between the mouth and bile ducts there is a distinct bend in the digestive tube. At this point there is no marked change in the nature of the lining epithelial cells, although it is to be noted that the tube posterior to the bend is of smaller caliber, and the ridges are distinctly fewer in number (compare Figs. 2, 4 of Pl. X).

Despite the fact that the lining cells on either side of the "bend" resemble each other to a marked degree, it nevertheless appears probable that at this point the esophagus ends and the stomach begins. As a matter of fact there is but little change in the character of the epithelium between the mouth and the bile ducts. The digestive tube enlarges considerably between the bend and liver ducts, but otherwise there are no especially distinctive features. However, it is important to note in this respect that in all of the *Arcidae* there is a distinct section between the bile ducts and the undoubted esophagus. This interval, to be sure, varies in extent, but invariably it is present. In this species, therefore, it appears that the most reasonable solution of the problem is to assume that the union of the esophagus and stomach is located at the point where the bend appears.

Posterior to the bile ducts the stomach becomes a more complicated organ with walls composed of cells of varying heights and fashioned into ridges too complicated to reconstruct. The lower division of the stomach is provided with ridges which may correspond to those responsible for the secretion of the crystalline stile in other species, but here they never are prominent (see right side of stomach on Pl. IX, Fig. 8).

An unusual development exists in the gastric epithelium covering approximately one-third of the right side of the lower division of the stomach (Pl. IX, Fig. 8). Throughout this area the component cells are low cubical elements in marked contrast to their surrounding neighbors. Anteriorly it is bordered by a distinct ridge which extends from the intestine to the junction of the two divisions of the stomach. Posteriorly it shades gradually into the usual type of epithelium.

The configuration of the upper division of the stomach is determined to an unusual degree by ducts from the digestive gland. At not less than thirty points the gastric epithelium forms distinct diverticula, each of which unites with secreting follicles. On the right side of the stomach these are relatively few in number (Pl. XI, Fig. 6), and thus are in marked contrast to those extending across the ventral surface of the stomach and up its left face. This last named group is shown uniting with the stomach in a successive series of sections (Pl. X, Figs. 9, 10, 12). Also in diagrammatic fashion these are shown on Pl. X, Fig. 1.

The intestine at a point nearest to the mouth is slightly more complicated than in *Arca*, but otherwise its course is essentially the same. Unlike *Arca*, however, the heart surrounds the gut (Pl. XI, Fig. 10). Throughout its entire extent a typhlosole is present in the intestine, its general form being represented on Pl. IX, Fig. 8. As usual the anal opening is on the ventral surface of the posterior adductor.

Attention already has been called to the fact that the gut penetrates the heart, and in a more detailed fashion this fact is indicated on Pl. XI, Fig. 10. As is there indicated, there is but a single pericardial cavity, and distinct valves guard the auriculo-ventricular openings. Anteriorly the ventricle or ventricular outpouchings give rise to a large anterior aorta. This same figure, together with that of Pl. XV, Fig. 1, also shows that there is a similar broad union ventral to the intestine. Evidently this union is due to a fusion of the outpouchings and not to the enlargement of the ventral vessels responsible for the formation of the posterior aorta. As may be seen these vessels are clearly defined, and hold essentially the same position as in other species represented on the same plate.

The urogenital system in this species is exceptionally clearly defined, the greater number of its principal features appearing in a single section (Pl. X, Fig. 8). Here the external opening leads into an atrium which on one hand leads into the genital duct and at the same level connects with the ciliated reno-pericardial canal and a passage into the main kidney cavity as well. No attempt was made to reconstruct the shape of the entire kidney, but a cross section (Pl. XI, Fig. 3) shows the organ to be somewhat triangular in outline with a thin-walled, apparently non-glandular roof to the secreting follicles of the other two sides.

Anadara

In this genus *A. bisenensis* and *A. granosa* are regarded as typical species. As may be learned from the figures, the external features of both are essentially the same (compare Pl. XIII, Fig. 1, and Pl. XIV, Fig. 7). The mantle in *A. bisenensis* is highly glandular, much less so in *A. granosa*. Another difference affects the size of the palps which in part may be due to shrinkage. In *A. bisenensis* the abdominal sense organs vary to a considerable degree as a comparison of Pl. XII, Fig. 5, and Pl. XIII, Fig. 10, will indicate. This difference may again be due to the action of the preservative. Evidently the Fig. 10 drawing represents the normal state of affairs since it is almost the exact copy of these organs in *A. granosa*. The byssus cavity in both species is of small size with walls delicately ridged in *A. bisenensis* (Pl. XII, Fig. 9).

The digestive system of *A. bisenensis* is shown on Pl. XIII, Figs. 5, 6, that of *A. granosa* on Pl. XII, Fig. 10, and Pl. XIII, Fig. 2. From these figures it will be seen that there are no unusual features attaching to the esophagus, and in neither species is the stomach strikingly different. In each a marked diverticulum in the gastric wall occurs to the right of the esophageal opening, and, judging from gross dissection, its apex is firmly attached to the body wall. Furthermore, the removal of the connective tissue from the visceral cavity doubtless destroys some of the bile ducts, yet it is certain that, at least in *A. bisenensis*, ducts are attached to the antero-ventral gastric wall, and one or more open on the right side.

The intestine is markedly longer than in any species of the foregoing subfamily Arcinae, although in its general position there is an agreement. The chief difference concerns that section of the gut adjacent to the pedal ganglia which is thrown into several loops. It

passes to the ventral side of the pericardium as it makes its way to the under side of the posterior shell adductor.

The general appearance of the heart in both species is typified by the sketch of this organ in *A. bisenensis* (Pl. XIV, Fig. 3). A dye injected by means of a micropipette into the pericardial cavity on one side of the mid-line passed readily to the opposite side in this species, indicating a single cavity. The same method indicates that in *A. granosa* a connection exists, but evidently it is relatively of much smaller caliber. In *A. bisenensis* there is a well defined flap which may act as a valve at the junction of the ventricle and the anterior aorta (Pl. XII, Fig. 6).

The muscles of the visceral cavity of *A. granosa* are represented on Pl. XI, Fig. 12, of *A. bisenensis* on Pl. XII, Fig. 6. In this last named species there are two unique muscles which are inserted in the tissue surrounding the mouth opening. Both are unpaired strands, and the larger, extending across the visceral cavity, attaches a few of its fibers to the gastric wall in the neighborhood of the bile ducts (Pl. XII, Figs. 6, 8). The main bundle continues on to the junction of the two divisions of the stomach where it attaches to the gastric wall and to one of the ordinary transverse muscles. The smaller mate likewise extends across the visceral cavity, and is attached to one of the smaller transverse muscles.

Regarding the function of these muscles, it is difficult to form a reasonable explanation. Those fibers attached to the forward stomach wall may produce a dilation, possibly allowing of a freer flow of digestive fluid through the ducts, and a contraction of the main muscle may also dilate a portion of the stomach. Also those fibers attached to the transverse muscles may serve to enlarge the mouth opening or regulate in part the movements of the palps.

No especial study was made of the nervous, urogenital or circulatory systems.

Scapharca

This subgenus, embracing *S. auriculata*, *S. concinna* and *S. transversa*, has been established on the basis of a slight degree of asymmetry in the valves of the shell. This state of affairs, however, is not correlated with any other striking differences between this subgenus and typical species of *Anadara*. The mantle shows a weakly developed glandular differentiation adjacent to the umbones in *S. auriculata* and *S. transversa;* it is more pronounced in *S. concinna*. Other external features of the body are sufficiently represented to require no further comment (Pls. XI to XIV). The byssus cavity is weakly developed (Pl. XI, Fig. 11) with the exception of an unidentified species from the coast of Senegal, Africa, in which this organ is more complicated (Pl. VI, Fig. 10). The abdominal sense organs bear a close resemblance to those of *Anadara* s. s., a typical example being that of *S. auriculata* (Pl. XII, Fig. 7).

The digestive system presents no particular characters which separate this subgenus from typical anadaras. In every instance the esophagus is a simple tubular structure without any marked dilations or glandular developments. The stomach likewise is rather plain-walled in *S. auriculata* (Pl. XI, Figs. 4, 7) and *S. concinna* (Pl. XIII, Fig. 3). It is somewhat more complicated in *S. transversa* (Pl. XV, Fig. 5).

The intestine develops several loops in the neighborhood of the pedal ganglia, but possibly owing to their smaller body size these are less complicated (as in Pl. XII, Fig. 4) than in *Anadara* s. s. The gut passes by the ventral side of the pericardium to open

beneath the posterior adductor. The main muscles of the visceral cavity are represented on Pl. XII, Figs. 2, 3, and Pl. XIV, Fig. 9.

No sections were made of any of these species, but it has been determined that the pericardium is a single cavity in *S. concinna*.

Cunearca

On the basis of shell characters the three species, *C. chemnitzi*, *C. perlabiata*, and *C. incongrua*, are credited with a close relationship. From an anatomical standpoint this classification appears to be correct so far as the first two are concerned, but, as will be pointed out later on, there are certain differences which appear to throw some doubt upon the status of *C. incongrua*.

Externally all of these species exhibit the same general appearance (Pl. XIV, Fig. 4, Pl. XVI, Fig. 2, Pl. XVII, Fig. 5). The palps are nearly vertical or but slightly inclined, a statement even more accurate with respect to the upper half of the gills. A section through the palp of *C. perlabiata* is shown on Pl. XV, Fig. 8. The byssus is small in *C. chemnitzi* (Pl. XI, Fig. 11), and somewhat larger in *C. perlabiata* where a definite secretion has been developed (Pl. XIV, Fig. 4).

Elsewhere in this paper attention is called to the fact that in a genus or subgenus the various species exhibit a complex of characters which fundamentally are similar. And in this connection it is important to note that this also holds true with respect to the abdominal sense organs. In this subgenus *Cunearca* the three species possess these organs fashioned according to two patterns, and, as will be seen, there are two corresponding types of digestive tracts and of the transverse muscle bundles in the visceral cavity.

The first type of abdominal sense organ is present in *C. incongrua* (Pl. XVII, Fig. 3) where the anal opening and the region immediately anterior to it are bordered by delicate folds which may be sensory in character. The second type is present in *C. chemnitzi* (Pl. XV, Fig. 11) and *C. perlabiata* (Pl. XIV, Fig. 6). Here a fold, in the form of an arc, and located immediately behind the anal opening, has developed a conspicuous yet slender finger shaped projection in the mid-line.

The esophagus is comparatively short in *C. chemnitzi* and *C. perlabiata* (compare Pl. XIII, Fig. 8, and Pl. XV, Fig. 7). Also the stomach of these two species follows much the same pattern. In each a fold of the gastric wall is situated dorsally to the esophageal opening and one of the folds, coursing throughout the length of the ventral division of the stomach, terminates dorsally in a conspicuously developed knob. A very different picture appears in the case of *C. incongrua* (Pl. XVI, Fig. 1). Here the dorsal gastric fold holds a different position, and, although the ventral fold ends in a knob, the gastric epithelium presents an appearance unlike that in the other two species.

From these same figures it will be seen that the relative lengths of the intestines do not follow the rule according to which they should be of the same length in *C. chemnitzi* and *C. perlabiata*. As a matter of fact this organ is relatively short in the first named species, whereas in the other it is of approximately the same length as that of *C. incongrua*. In all three species the gut passes ventrally to the pericardium as it makes its way to the opening beneath the posterior adductor.

The pattern of the muscles bridging the visceral cavity is much the same in *C. chemnitzi* (Pl. XVI, Fig. 6) as in *C. perlabiata* (Pl. XVII, Fig. 1). The resemblance in the case of

C. incongrua is more remote (Pl. XVI, Fig. 3), the bundles in the region of the heart and those forming the posterior walls of the cavity being heavier than in any other species of the present collection.

As just noted, the heart is dorsal to the intestine. The pericardial cavity in *C. perlabiata* was found by the use of sections to be single and auriculo-ventricular valves were present. No sections were made of *C. chemnitzi*, but in the single individual examined on this point no dye injected on one side of the mid-line passed to the other side.

In *C. incongrua* the general appearance of the heart is practically the same as that of *C. perlabiata* (Pl. XIV, Fig. 11), and as in that species the pericardium is a single cavity. No sections were made of the other two species of this subgenus, but in *C. incongrua* the organs in the visceral cavity were imbedded in connective tissue so tough and resistant that a small specimen, 19 mm in length, was sectioned. In this manner it was discovered that the connective tissue "packing" was penetrated by a system of capillaries rather than by sinuses or lacunae of the usual type. Whether the term capillary is justified may be open to question. However, these vessels are clearly defined, and appear to possess definite walls. In any event each liver follicle is more or less surrounded by one or more of these channels, a condition that is unique, at least so far as the present collection is concerned.

The urogenital system of *C. perlabiata* was studied by means of sections, and, although the material was not well preserved, it appears that the general plan is similar to that of *Acar reticulata* (Pl. XV, Fig. 9), for example. There is no doubt that the duct from the kidney unites in the same fashion with the gonoduct, and close to this point of union the reno-pericardial funnel appears to enter the kidney.

Argina

Argina pexata is the sole representative of this genus, the individual figured on Pl. XVIII, Fig. 3, having a length of 52 mm. The mantle, especially in the region of the umbones, is highly glandular. The pedal furrow, averaging approximately 1 mm in depth, is smooth-walled throughout without any sign whatever of a byssus. The abdominal sense organs are shown on Pl. XVIII, Fig. 5.

The esophagus, as usual, is a tube of uniform caliber throughout, with an inner lining thrown into delicate longitudinal folds. The characteristics of both divisions of the stomach are sufficiently represented (Pls. XVII, Fig. 8, XVIII, Fig. 4, XIX, Fig. 3) to demand no further comment. Also these same figures show the complexity of the intestinal coils. Owing to the resistant character of the connective tissue in the visceral cavity, the bile ducts were detached, and hence their number and distribution are unknown. It is certain, however, that the gut penetrates the heart, and its outer opening is figured on Pl. XVIII, Fig. 5.

In the drawing of the muscular system spanning the visceral cavity it is to be noted that, with the removal of the digestive system and the associated connective tissue, the more delicate muscles were displaced. Therefore in the figure (Pl. XVIII, Fig. 6) only the more prominent muscles are represented.

As noted previously, the heart surrounds the intestine, and gives rise to the unpaired anterior (Pl. XIX, Fig. 1) and posterior aortae. The auricles ventrally are distinctly separated by a thin median partition. This partition, however, is incomplete, the two

division of the pericardial cavity communicating by a small foramen a short distance anterior to the pedal retractors.

No attempt was made to trace the circulatory system beyond this point, nor were the nervous or urogenital systems investigated.

Noetia

This genus is represented by a single species, *N. ponderosa*, the general external appearance of which is represented on Pl. XVIII, Fig. 1. The mantle is opaque and relatively thick due to the usual glandular development. The pedal furrow is comparatively shallow, and posteriorly terminates in a byssus cavity of small size with a small irregular median fold and corrugated roof. The abdominal sense organs are shown on Pl. XIX, Fig. 2.

The esophagus is flattened dorsoventrally, but otherwise is unmodified. The stomach, on the other hand, is unusually complicated (Pl. XVII, Fig. 11, and Pl. XVIII, Fig. 2). A gastric shield is present, having its main attachment with the dorsal fold near the anterior end of the stomach. Also in this particular specimen the stomach was entirely filled with crystalline stile secretion which obscured the finer details of the gastric epithelium.

Bile ducts open through the antero-ventral gastric wall, and also on the right at about the same level. At these points there are small conical papillae (Pl. XVII, Fig. 11), but whether the ducts actually open through them could not be determined satisfactorily.

The general appearance of the heart is shown on Pl. XVII, Fig. 7. A definite septum separates the pericardium dorsal to the intestine, and dye injected into the cavity did not cross the mid-ventral line. It thus appears that two cavities exist. The dorsal aorta courses anteriorly to the right of the mid-line as far as the pedal protractor, and, after supplying a small branch to the cerebral ganglia, it ramifies throughout the visceral cavity.

The musculature of the visceral cavity is represented on Pl. XXI, Fig. 9. From this it is evident that in this respect the genus *Noetia* does not appear to be very closely related to other species in the present collection.

No serious attempt was made to trace the various branches of the nervous system, or to determine the relations of the urogenital system. It may be added, however, that an unusual feature occurs in connection with the reproductive system where a portion of the gonad occupies spaces among the fibers of the pedal retractor in the region of the "heel."

Cucullaea

Cucullaea granulosa is represented in the present collection by a single individual 70 mm in length. Its main external features are represented on Pl. XVI, Fig. 4. The mantle is unusually transparent, and evidently lacks the glandular development characteristic of the average arcid. The abdominal sense organs are illustrated on Pl. XX, Fig. 9. The foot is traversed by a longitudinal groove throughout the greater extent of its ventral face. Near the "heel" of the foot the wall of the byssus cavity is fashioned into a small yet distinct median fold bounded externally by three others of much smaller size (Pl. XVII, Fig. 10, and Pl. XIX, Fig. 5). This is in essential agreement with Pelseneer's description and figure in the Siboga report.

The esophagus is a relatively simple tube, thick walled, and internally is provided with a series of longitudinal folds. The stomach likewise presents a comparatively unmodified appearance both externally and internally (Pl. XIX, Fig. 6, Pl. XXI, Fig. 8).

In the present specimen the dorsal gastric division was laterally much compressed, and to the right of the esophageal opening there was a deep lateral pocket the blind end of which was firmly anchored to the body wall. The gastric epithelium of the lower division of the stomach was folded into seven longitudinal ridges. It may be added that both divisions of the stomach were completely filled with crystalline stile secretion. Also one bile duct opened on the left face of the stomach (Pl. XXI, Fig. 8), two were more ventrally placed near the mid-line of the body, while a third was situated about the middle of the right gastric wall.

The intestine, upon leaving the stomach, courses anteriorly and in the neighborhood of the pedal ganglia turns sharply upon itself and, in close contact with the right side of the stomach, makes its way to the pericardium where it is surrounded by the heart. Its opening upon the ventral surface of the shell adductor is represented on Pl. XX, Fig. 9.

The main features of the musculature in the greater number of species treated in the present work conform to a broad general plan. Hence, in order to avoid unnecessary repetition, the muscular system of *Cucullaea granulosa* is herewith described in some detail, and only exceptions to the rule will be noted in the description of other species.

The dorsal wall of the body, between the pedal protractors and the pericardium, is reinforced by a series of more or less transverse muscle bundles (Pl. XX, Fig. 12). In dissections these are seen to be continued laterally, and to share in the formation of the lateral body wall. Less conspicuous in surface view are several muscle bundles which are inserted in the dorsal body wall close to the mid-dorsal line. These ventrally break up into a series of radiating fibers, and, extending across the visceral cavity, also form a portion of the lateral body wall.

Owing to the large size of this species, a more than usual amount of care has been taken to examine the muscular system in the region of the mouth. As usual, the esophagus itself is supplied with circular and longitudinal fibers. The dorsal palp appears to be operated by, first, a delicate offshoot from the pedal protractor, and, secondly, there is a well developed muscle which on one hand radiates, and attaches to the body wall into which it is incorporated, while the other extremity is inserted in the region immediately in front of the palp, at the same time sending a small number of strands into the palp itself. Evidently the main function of these muscles is to elevate the oral region, and thus perhaps cooperate with the esophageal muscles in forcing the food onward toward the stomach.

In addition to the above described muscles there are numerous filaments radiating from the esophagus in the oral region some of which are inserted in the body wall, while others extend in among the follicles of the digestive gland where evidently they are anchored to the connective tissue. Obviously the function of these strands is to increase the caliber of the esophagus.

The transverse muscles bridging the visceral cavity are represented on Pl. XX, Fig. 12. It is to be noted that one, highly irregular in shape and situated immediately behind the oral region, gives rise to a single strand (not figured) that, as in *Anadara bisenensis* (Pl. XII, Fig. 8), makes its way to the stomach wall. In *A. bisenensis* some of the fibers attach to the anterior gastric wall while the main cord passes on to the junction of the two divisions of the stomach. In the present case it is not certain that any fibers pass to the anterior regions of the stomach, but otherwise the two species are similar in this respect.

The pericardium and heart of this species are represented on Pl. XV, Fig. 10, and Pl. XIX, Fig. 4. The ventricle surrounds the intestine, and the aortae originate in normal fashion. Each auricle, it may be added, extends to the mid-ventral line of the pericardium, thus terminating in a cul-de-sac.

The details of the nervous and urogenital systems were not determined.

Glycymeris

This genus is represented by four species, *G. americana*, *G. migueliana*, *G. longior* and *G. subobsoleta*. These form a closely related group, the only differences appearing to be those relating to minor details. In every instance eye spots occur on the mantle border throughout the posterior half. The foot is well developed, and is provided with a shallow plain walled groove. No microscopical sections were made, but macroscopically there are no evidences of a definite glandular development. The palps differ considerably in relative size, due possibly to contraction in the preservative, and the characteristic grooves are faint even in stained preparations.

The digestive system in all of the species is constructed upon essentially the same plan. In some individuals there are slight variations, such as the presence or absence even in the same species, of the delicate radiating grooves in the upper division of the stomach (as in Pl. XIX, Figs. 7, 8), but otherwise there are no important differences.

The esophagus is compressed dorso-ventrally, and the lining epithelium is fashioned into a series of delicate longitudinal folds. At no point is there a noticeable enlargement or any indication of glandular development suggestive of the pharyngeal cavity in other classes of mollusks.

The general appearance of the stomach of the various species is represented on Pls. XIX, XX, XXI. In *G. subobsoleta* the ventral division of the stomach is smooth walled, or is provided with one or two very small longitudinal folds. In the other species these folds usually are more conspicuous, but even here the variation may be considerable. In most instances the lower gastric section contained an abundance of crystalline stile secretion.

One bile duct, ventrally situated anterior to the junction of the two divisions of the stomach, is universally present. In *G. subobsoleta* a second duct opens behind the union of the esophagus and stomach. In *G. longior* a single duct opens at approximately the center of the right side of the stomach. In *G. americana* there are two ducts in the same position.

The intestine is comparatively short, and in most instances its form and location resemble that occuring in *Arca*. Its most complicated development appears in *G. americana* (Pl. XXI, Fig. 5). In every case the heart surrounds the gut.

The musculature presents no noteworthy features with the possible exception of the transverse muscle bands spanning the visceral cavity. In the two smaller species, *G. migueliana* and *G. subobsoleta*, these are relatively slender and delicate, whereas in *G. americana* and *G. longior* they are unusually well developed. In another connection (Heath '37) it was suggested that by the contraction of this set of muscles the volume of the visceral cavity is decreased, and that a portion of the blood in the visceral sinuses is thus forced into the foot. Hence these muscles serve indirectly as pedal protractors. Their development, therefore, may be correlated with body size and weight and possibly with the nature of the sea bottom over or through which the animal progresses.

At this stage attention is called to the fact that several species in the present collection possess muscles, usually extremely delicate which are attached to the stomach, and usually are inserted in the body wall. However, owing to their delicacy, and the tenacious connective tissue of the visceral cavity, it usually is impossible to carry on ordinary dissection without dislodging these strands. In *G. subobsoleta* the connective tissue is weak, and the major portion of these gastric muscles is represented on Pl. XXI, Fig. 4. They doubtless act as dilators.

The abdominal sense organs vary to a slight degree. What appears to be the typical condition occurs in *G. americana* (Pl. XXI, Fig. 6) and *G. migueliana* (Pl. XX, Fig. 10). In both of these species the rectum extends beyond the level of the sense organs, a state of affairs differing from that of *G. longior* (Pl. XX, Fig. 5).

Résumé

According to Reinhart's classification ('35), the family Arcidae includes three subfamilies. The first, Arcinae, embraces, so far as the present collection is concerned, Arca, Barbatia, Arcopsis, Bathyarca and Trisodos. The second subfamily, Anadarinae, is represented by Anadara, while Noetia is included in the subfamily Noetiinae.

In an attempt to determine to what extent this scheme of classification actually represents phylogenetic relationships it has become increasingly evident, as Pelseneer emphasized years ago, that we must carry our investigations to a greater length than exists at present. In this family, the Arcidae, not over a dozen species have been investigated up to the present time, and nowhere is there any information regarding their development. Nevertheless various theories have been proposed to account for the phylogeny of this and related families, or for the origin of certain anatomical features, and while most of these theories may be discarded at a later date they are valuable aids in focussing attention upon the more important problems in need of solution. As Weismann remarked, "the way to truth is often through inevitable error," and with this dictum in mind various data are presented in the following paragraphs which it is hoped may lead to a truer knowledge of the group.

During the course of the present work it became evident (as it has to other investigators) that classification on the basis of a single character or individual system of organs may lead to faulty conclusions. Obviously where only fossil remains are available classification cannot be otherwise, but where living representatives are available, shell characters and the internal anatomy should be treated as a unit. The validity of this line of reasoning is indicated in the case of *Arca imbricata*, for example. Here is a species, represented by two individuals, the shell characters of which are declared to be identical and to be typical species of the genus. From the standpoint of their internal anatomy they are unlike. Also from conchological criteria three species have been included in the subgenus Cunearca. Anatomically it is certain that one of these is incorrectly included. In the same category is Acar pernoides which differs materially from other species of the genus.

But while there is no obvious objection to the plan of including a study of the internal anatomy together with the shell characters, there are certain difficulties. As all students of the subject are well aware, some systems of organs are more subject to modification than others. And what adds to the difficulty is the fact that the range of variation in one subgenus or genus is greater than in another. Hence, as usual, the interpretation of the data and the formulation of a scheme of classification become matters of personal judgment.

However, it appears to be fairly well established that in the family Arcidae the urogenital system is constructed upon much the same plan throughout. Also it seems equally certain that the nervous system is highly conservative, undergoing slight changes only in the various included species. Possibly *Acar pernoides* may prove to be an exception. But while this may be the case it apparently does not apply to some of the sense organs which it supplies. Pelseneer ('11) in his study of the "eye spots" of various pelecypods has shown that, at least broadly, these structures aid in the formulation of a scheme of classification. Furthermore, in several instances in the present study, where the general internal anatomy indicates the generic or subgeneric rank of certain species, the abdominal sense organs exhibit a close resemblance. To what extent these structures may be relied upon in tracing relationships remains in doubt at present, but most emphatically they merit further investigation.

Furthermore, considerable doubt exists at present with respect to the byssus as a distinguishing feature in classification. In some instances it appears to be of value when it is considered along with other organs of the body. In other cases its value is doubtful. The question calls for a broader survey before its true worth can be determined. The same line of reasoning applies to the transverse muscles spanning the visceral cavity. In some species these are of such a distinctive size, or their distribution is such that together with other organs of the body they doubtless should be taken into consideration.

A buccal or pharyngeal cavity may have been present in the ancestral pelecypod, but so far as the present collection is concerned its existence is doubtful indeed. In some individuals there were slight dilations in the region of the mouth or at varying points between the mouth opening and the stomach, but in other specimens of the same species no trace of these existed. Furthermore, the epithelial lining throughout was of uniform character, and where sectioned material was available the same types of cells occurred throughout. Where gland cells existed these, with the exception of *Acar pernoides*, were evenly distributed, or where they were more abundant in the mouth region their numbers gradually lessened as the stomach was approached. In short, no definite buccal region was distinguished.

In the present work various other features of the digestive system have been investigated, but it should be noted that the results largely are based upon gross dissection. Where histological methods are employed the results may disclose resemblances and differences of value in classification; but at present this system appears to be relatively plastic, some species even in the same subgenus exhibiting marked differences. However, there are indications that the length of the intestine may serve, in some instances at least, to distinguish subfamilies. For example, this organ is comparatively short throughout the entire subfamily Arcinae, whereas it is of greater length and more contorted in the Anadarinae.

The number and distribution of the bile ducts likewise may aid in the classification of subfamilies or even subgenera. In gross dissection these structures are so delicate and so readily dislodged that in a few species only have their exact number and position been determined.

In a few cases a gastric shield is known to exist, and in several others it appeared to be present. In the majority of the specimens the crystalline stile secretion coated the lining of the dorsal division of the stomach to such an extent that if any shield did exist its presence

could be detected only after sectioning. The value of this structure in classification is therefore an unknown quantity.

In this family the pericardium and heart have been the subject of investigation and discussion to a greater extent, excluding the shell, than any other organs of the body. From the time of Poli (1795), who discovered the paired hearts of *Arca*, until the present time a very considerable number of investigators have published studies along this line, so that now we have a fairly accurate picture of these organs in approximately a dozen species. The whole subject is adequately reviewed in the works of Theiler ('07) and Matthias ('14). A few additional items included in the next paragraphs are based upon findings during the course of the present work.

That *Arca noae*, for example, has a double heart no one denies. But there are numerous species in which it is difficult to decide whether the heart is a single chamber with lateral dilations of the ventricle or whether it actually is double. Theiler cuts the Gordian knot between the stage where there are two pericardial cavities on one hand and a single one on the other. A paired pericardium indicates a double heart, a single cavity an unpaired heart. And this appears to be the best line of cleavage that any one has proposed.

No doubt exists as to the dorsal position of the heart with reference to the intestine in those species of Arcidae with a single heart, and in species, such as *Arca noae* or *Barbatia barbata*, the heart is still considered to be dorsal although a ventricular bridge is lacking. In this latter case the junction is accomplished by the union of two aortae the fusion of which in the mid-line results in the formation of the anterior aorta; and in the same fashion the ventral aorta is formed by the union of two aortae.

Furthermore, in those more highly specialized species the dorsal aortae appear unquestionably to be arterial in character since they resemble undoubted arteries elsewhere in the body. On the other hand, the ventral aortae are not so sharply differentiated. As various authors have noted, this ventral system, as it leaves the ventricles or ventricular pouches, is often difficult to trace since the lumina are crossed by muscle fibers the general appearance and arrangement of which suggest that actually they are ventricular elongations rather than definite blood vessels. And this appearance on occasion is heightened when the vessels are gorged with blood. In *Arcopsis adamsi*, for example, the ventral vessels in one specimen were so distended with blood that it appeared to be certain that the gut penetrated the heart. In two other individuals subsequently examined the heart was of the usual type (Pl. VIII, Fig. 8).

In this connection it is interesting to note the state of affairs in *Trisodos tortuosa*. In this species the pericardium is a single cavity (Pl. XI, Fig. 10), and the heart surrounds the intestine, and, it may be added, the dorsal bridge uniting the ventricular pouches is of the same size as the ventral union shown of Pl. XV, Fig. 1. Furthermore, it is a significant fact that the ventricular pouches have fused ventral to the gut, and in the process the roots of the ventral aorta have retained their individuality. In other words, it appears to be certain that these last named vessels are actual arteries.

At the present time it appears to be a futile undertaking to account for the double heart in Arca, or to decide whether it represents a primitive state or not. It is generally agreed that it occurs in those species in which the pedal retractors have become greatly developed, thus increasing the width of the body. During this process the gills and their attendant sinuses have been drawn farther and farther away from the mid-line. In such

fashion various authors account for the gradual lateral extension of the heart and its final separation into two distinct divisions. According to this view the double heart has been derived from a single one. On the other hand there are others, notably Milne-Edwards and Thiele, who consider that the paired heart is the more primitive.

In the present collection there is a definite relation in *Arca* s. s. between the size of the retractors and the degree of separation of the ventricles. The larger the muscles the wider the gap. And it appears reasonable to go a step farther in directing attention to the fact that the size of these muscles is correlated with the development of the byssus. Furthermore, it scarcely can be argued that in mollusks at least a sessile state is a primitive condition. Accordingly it would logically follow that the pedal retractors were of smaller size in the ancestral types, and the width of the body was relatively less. From which it may be argued further that the type of heart in *Barbatia*, for example, more closely resembles an ancestral condition than it does in a typical *Arca* such as *A. noae*. However, these are pure assumptions; we need facts, many more than we have at present.

Matthias has discussed exhaustively the various theories to account for the phylogenetic beginnings of the arcid heart, and the present data add little if anything to the subject. All that we know at the present time is based upon not more than a dozen species, and also we have no assurance that comparisons with other classes of mollusks or annelids are legitimate. Moreover, we have no assurance that the development of a freshwater species, such as *Cyclas cornea* of *Nucula delphinodonta*, a protobranch, follows the same course as that of Arca the development of which is unknown. Until we have such information, and a wider view of filibranch anatomy, it would appear that our theorizing is little more than a mental exercise.

The more significant differences between the various species are included in the following paragraphs. The most striking of these occurs in the case of *Arca imbricata* and *A.* sp., as detailed in the main body of the text. The four other species in the present collection are typical arcids.

The genus *Barbatia* is represented by two typical species, *B. barbata* and *B. decussata*. Three species, *gradata*, *reticulata* and *pernoides*, are included in the subgenus *Acar*. According to some authors the first two are believed to be conspecific. Reinhart ('39) argues against this point of view, and in the present work (page 296) evidence is presented which supports his claim. This same author also maintains that in the case of *A. pernoides* there are slight differences between its shell and that of *A. gradata*, and that they are distinct species. This certainly is a legitimate conclusion, for *A. pernoides* is quite different from any other species in the present collection. Reinhart ('35) also states that *Cucullaerca*, from the standpoint of shell structure, "comprises a clearly recognizable group." Its internal organization, however, resembles that of *B. barbata*.

The genus *Arcopsis* is clearly defined, and distinct from other genera in the family. *Bathyarca*, represented by *B. pectunculoides*, is equally sharply demarcated. The genus *Trisodos*, with its remarkable asymmetry and unusual type of stomach and heart, is even more distinct and remote from other genera in the family.

The subfamily Anadarinae is represented by the genus *Anadara* of which there are two typical species, *A. bisenensis* and *A. granosa*. Owing to a slight asymmetry in the valves of the shell, the subgenus *Scapharca* has been established with its members in the present collection comprising *S. auriculata*, *S. concinna* and *S. transversa*. However,

from the standpoint of their internal anatomy these three species ordinarily would be considered to be typical members of the genus.

The subgenus *Cunearca* is credited with three species in the present list, *C. chemnitzi*, *C. perlabiata* and *C. incongrua*. Anatomically the first two are typical, but the status of *incongrua* is open to doubt. Fundamental differences between the two groups are detailed in the description of the subgenus.

Noetia ponderosa is the sole species belonging to this genus. It does not appear to be closely allied to other species in the family.

At the suggestion of Doctor H. G. Schenck, *Cucullaea granulosa* and a few members of the genus *Glycymeris* are included in the foregoing descriptions. Their relationship to the Arcidae is obscure.

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EXPLANATION OF PLATES

PLATE I

FIG. 1. *Arca* sp., length 84 mm.
FIG. 2. *Arca* sp., ventral view of anterior end of body.
FIG. 3. *Arca* sp., byssus cavity, × 1.5.
FIG. 4. *Arca* sp., lateral view, × 1.
FIG. 5. *Arca* sp., section through gonad.
FIG. 6. *Arca* sp., dorsal view of cerebro-pedal system; *a*, border of shell adductor sheath; *m*, mantle nerves.
FIG. 7. *Arca* sp., right half of body, lateral view.
FIG. 8. *Arca* sp., section through one of the gonad tubules.

PLATE II

FIG. 1. *Arca* sp., right half of digestive system, × 5.
FIG. 2. *Arca* sp., left half of digestive system, × 5.
FIG. 3. *Arca* sp., visceral ganglia and nerves, × 4; *b*, branches on dorsal body wall; *g*, pair of nerves to gills; *m*, mantle nerves; *s*, nerve to abdominal sense organ.
FIG. 4. *Arca* sp., posterior end of body.
FIG. 5. *Arca noae*, follicles of gonad.
FIG. 6. *Arca* sp., gonad tubules.
FIG. 7. *Arca* sp., nervous system of left mantle lobe.
FIG. 8. *Arca bouvieri*, dorsal view, × 2.

PLATE III

FIG. 1. *Arca zebra*, × 1.5. The anterior end is slightly widened.
FIG. 2. *Arca zebra*, right side of digestive system, × 4; *r*, pedal retractor. Locality, North Carolina.
FIG. 3. *Arca zebra*, right side of digestive system, × 4. Locality, Porto Rico.
FIG. 4. *Arca zebra*, left side of body, length, 60 mm.
FIG. 5. *Arca noae*, left side of stomach, × 4.
FIG. 6. *Arca bouvieri*, ventral view of anal region, × 5.
FIG. 7. *Arca pacifica*, ventral view of anal region, × 6.
FIG. 8. *Arca noae*, right side of digestive system, × 4; *r*, pedal retractor.
FIG. 9. *Arca zebra*, ventral view of anal region, × 3.

PLATE IV

FIG. 1. *Arca pacifica*, lateral view, length, 82 mm.
FIG. 2. *Arca bouvieri*, right half of digestive system, × 3; *r*, pedal retractor.
FIG. 3. *Arca pacifica*, dorsal view.
FIG. 4. *Arca umbonata*, right half of stomach, × 5; *r*, pedal retractor.
FIG. 5. *Arca umbonata*, left half of stomach, × 5.
FIG. 6. *Arca umbonata*, dorsal view, × 2.
FIG. 7. *Barbatia candida*, dorsal view, × 2.
FIG. 8. *Arca bouvieri*, left side of digestive system, × 4; *r*, pedal retractor. Another specimen Fig. 2, Pl. iv.
FIG. 9. *Arca pacifica*, right side of stomach, × 5.
FIG. 10. *Barbatia decussata*, dorsal view, × 2.
FIG. 11. *Arca bouvieri*, byssus cavity, × 3.
FIG. 12. *Arca zebra*, byssus cavity, × 4.

PLATE V

FIG. 1. *Barbatia decussata*, × 2.
FIG. 2. *Barbatia barbata*, × 2.

FIG. 3. *Arca pacifica*, left side of stomach, × 5.
FIG. 4. *Barbatia candida*, right side of stomach, × 4.
FIG. 5. *Barbatia candida*, left side of stomach, × 4.
FIG. 6. *Anadara granosa*, × 2. Abdominal sense organs.
FIG. 7. *Barbatia barbata*, dorsal view, × 2.
FIG. 8. *Barbatia decussata*, muscles of visceral cavity, right side, × 4.
FIG. 9. *Barbatia pernoides*, abdominal sense organs, × 5.
FIG. 10. *Barbatia barbata*, abdominal sense organs, × 5.

PLATE VI

FIG. 1. *Barbatia reticulata*, lateral view; length, 13 mm.
FIG. 2. *Barbatia decussata*, lateral view of digestive system, × 8.
FIG. 3. *Barbatia decussata*, right half of body, × 3.
FIG. 4. *Barbatia reticulata*, dorsal view of cerebro-pedal nervous system, a reconstruction; *a*, nerve to anterior shell adductor; *m*, mantle nerves; *o*, otocyst.
FIG. 5. *Barbatia reticulata*, dorsal view of visceral ganglia and nerves, a reconstruction; *d*, nerve to dorsal surface of the body; *g*, nerve to gill; *m*, mantle nerves.
FIG. 6. *Acar pernoides*, dorsal view, × 5.
FIG. 7. *Acar pernoides*, section through stomach and bile ducts posterior to Pl. VII, Fig. 1, and along line *b*, Pl. VII, Fig. 11.
FIG. 8. *Acar pernoides*, longitudinal section through kidney and gonoduct; *a*, pericardial cavity; *s*, gonad.
FIG. 9. *Barbatia reticulata*, reconstruction of digestive system.
FIG. 10. *Barbatia decussata*, byssus cavity, ventral view, × 4.

PLATE VII

FIG. 1. *Acar pernoides*, section through stomach and bile ducts anterior to Pl. VI, Fig. 7, and along line *a*, Pl. VII, Fig. 11.
FIG. 2. *Arcopsis adamsi*, median longitudinal section.
FIG. 3. *Arcopsis adamsi*, section through bile ducts.
FIG. 4. *Arcopsis solida*, abdominal sense organs, × 10.
FIG. 5. *Barbatia decussata*, dorsal view, × 2.
FIG. 6. *Arcopsis solida*, dorsal view, × 3.
FIG. 7. *Arcopsis solida*, left half of stomach.
FIG. 8. *Barbatia reticulata*, reconstruction of heart, dorsal view.
FIG. 9. *Barbatia candida*, main muscles of visceral cavity, × 5.
FIG. 10. *Arcopsis solida*, lateral view, × 4.
FIG. 11. *Acar pernoides*, median longitudinal section through anterior end of body. *a*, *b* correspond to Pl. VII, Fig. 1, and Pl. VI, Fig. 7.

PLATE VIII

FIG. 1. *Arcopsis adamsi*, section through heart; *i*, intestine.
FIG. 2. *Arcopsis adamsi*, reconstruction of digestive system; *a*, indicates position of Fig. 3, Pl. VII; *b*, that of Fig. 14, Pl. VIII.
FIG. 3. *Bathyarca pectunculoides*, reconstruction of stomach and bile ducts, ventral view.
FIG. 4. *Bathyarca pectunculoides*, cross section through palp region; *g*, gonad; *p*, palp.
FIG. 5. *Bathyarca pectunculoides*, cross section in region of rectum; *d*, circular disc of modified epithelium, possibly glandular; *f*, mantle fold shown in Fig. 15; *r*, rectum.
FIG. 6. *Arcopsis adamsi*, reconstruction of heart and sub-intestinal loop.
FIG. 7. *Bathyarca pectunculoides*, cross section through anterior end of foot.
FIG. 8. *Arcopsis solida*, lateral view of digestive system.
FIG. 9. *Arcopsis solida*, cross section through byssus region.

FIG. 10. *Bathyarca pectunculoides*, cross section through byssus represented by heavy irregular line; *i*, intestine; *r*, gonad.

FIG. 11. *Bathyarca pectunculoides*, reconstruction of digestive system.

FIG. 12. *Bathyarca pectunculoides*, cross section through abdominal sense organ, *s*, and *r*, rectum.

FIG. 13. *Arcopsis adamsi*, external layer of mantle, showing glandular development.

FIG. 14. *Arcopsis adamsi*, cross section of stomach and bile ducts, corresponding to line *b*, Fig. 2, Pl. VIII.

FIG. 15. *Bathyarca pectunculoides*, ventral view of posterior end of body.

PLATE IX

FIG. 1. *Bathyarca pectunctuloides*, section through middle of oesophagus.

FIG. 2. *Bathyarca pectunctuloides*, median longitudinal section through body.

FIG. 3. *Bathyarca pectunculoides*, cross section of pedal furrow between Figs. 7 and 10, Pl. VIII; *i*, intestine; *s*, gonad.

FIG. 4. *Bathyarca pectunctuloides*, cross section near posterior end of body.

FIG. 5. *Trisodos tortuosa*, reconstruction of digestive system, right hand face.

FIG. 6. *Bathyarca pectunculoides*, lateral view, × 8.

FIG. 7. *Trisodos tortuosa*, lateral view, × 1.3.

FIG. 8. *Trisodos tortuosa*, cross section near middle of stomach. *b*, dorsal aorta; *c*, liver; *d*, bile ducts; *g*, gonad.

PLATE X

FIG. 1. *Trisodos tortuosa*, reconstruction of digestive system; letters indicate position of sections shown in other figures.

FIG. 2. *Trisodos tortuosa*, cross section of stomach along line *c*, Fig. 1.

FIG. 3. *Trisodos tortuosa*, cross section of oral opening, *m*, and palps, *p*.

FIG. 4. *Trisodos tortuosa*, cross section of oesophagus along line *b*, Fig. 1.

FIG. 5. *Trisodos tortuosa*, cross section of palps.

FIG. 6. *Bathyarca pectunculoides*, cross section of heart; *i*, intestine.

FIG. 7. *Bathyarca pectunculoides*, cross section of stomach and bile ducts.

FIG. 8. *Trisodos tortuosa*, cross section at level of external urogenital opening; *a*, auricle; *c*, pericardium; *r*, kidney; *s*, blood sinus.

FIG. 9. *Trisodos tortuosa*, first of three successive cross sections through bile ducts along line *d*, Fig. 1, Pl. X.

FIG. 10. *Trisodos tortuosa*, section through bile ducts immediately behind Fig. 9.

FIG. 11. *Trisodos tortuosa*, cross section through kidney slightly anterior to Fig. 8; *a*, auricle; *c*, pericardium; *g*, gonoduct; *n*, cerebro-pedal connective; *r*, kidney; *s*, blood sinus.

FIG. 12. *Trisodos tortuosa*, cross section of stomach immediately behind Fig. 10, Pl. X.

FIG. 13. *Trisodos tortuosa*, dorsal view, × 1.3.

PLATE XI

FIG. 1. *Trisodos tortuosa*, ventral view of rectum and abdominal sense organs.

FIG. 2. *Anadara auriculata*, lateral view, × 1.3.

FIG. 3. *Trisodos tortuosa*, cross section of main portion of kidney.

FIG. 4. *Anadara auriculata*, left half of digestive system, × 4.

FIG. 5. *Trisodos tortuosa*, ventral view of byssus cavity, × 4.

FIG. 6. *Trisodos tortuosa*, cross section through stomach and bile ducts along line *e*, Pl. 10, Fig. 1.

FIG. 7. *Anadara auriculata*, right half of digestive system, × 4.

FIG. 8. *Anadara concinna*, dorsal view, × 2.

FIG. 9. *Anadara auriculata*, dorsal view, × 2.

FIG. 10. *Trisodos tortuosa*, cross section through ventricle surrounding the gut; auriculo-ventricular valves present; cerebro-visceral connectives, gonoducts and foot shown ventral to heart.

FIG. 11. *Anadara concinna*, byssus cavity, × 4.

FIG. 12. *Anadara granosa*, main muscles of visceral cavity, × 3.

PLATE XII

FIG. 1. *Anadara concinna*, lateral view, × 2.5.
FIG. 2. *Anadara concinna*, muscles of visceral cavity, × 5.
FIG. 3. *Anadara auriculata*, muscles of visceral cavity, × 5.
FIG. 4. *Anadara auriculata*, intestinal loops, left side.
FIG. 5. *Anadara bisenensis*, rectum and abdominal sense organs, × 4.
FIG. 6. *Anadara bisenensis*, muscles of visceral cavity.
FIG. 7. *Anadara auriculata*, rectum and abdominal sense organs, × 4.
FIG. 8. *Anadara bisenensis*, intestinal loops, bile ducts, *b*, and muscle, *m*, attached to gastric wall.
FIG. 9. *Anadara bisenensis*, byssus cavity, × 5.
FIG. 10. *Anadara granosa*, left half of stomach, × 4.
FIG. 11. *Barbatia gradata*, byssus cavity, right side, × 4.

PLATE XIII

FIG. 1. *Anadara granosa*, lateral view, × 2.
FIG. 2. *Anadara granosa*, digestive system viewed from left side, × 4.
FIG. 3. *Anadara concinna*, digestive system viewed from left side, × 5.
FIG. 4. *Anadara concinna*, rectum and abdominal sense organs, × 4.
FIG. 5. *Anadara bisenensis*, digestive system, × 3.
FIG. 6. *Anadara bisenensis*, left half of stomach, × 3.
FIG. 7. *Anadara transversa*, dorsal view, × 3.
FIG. 8. *Cunearca perlabiata*, digestive system, × 2.
FIG. 9. *Anadara gradata*, length, 22 mm.
FIG. 10. *Anadara bisenensis*, abdominal sense organs, × 3.

PLATE XIV

FIG. 1. *Anadara transversa*, × 2.
FIG. 2. *Barbatia gradata*, length, 24 mm.
FIG. 3. *Anadara bisenensis*, × 1.5.
FIG. 4. *Anadara perlabiata*, × 1.
FIG. 5. *Anadara transversa*, abdominal sense organs, × 6.
FIG. 6. *Anadara perlabiata*, abdominal sense organs, × 4.
FIG. 7. *Anadara bisenensis*, × 1.
FIG. 8. *Barbatia reticulata*, cross section through anterior portion of foot.
FIG. 9. *Anadara transversa*, main muscles of visceral cavity, × 4.
FIG. 10. *Barbatia reticulata*, section through byssus cavity; *i*, intestine.
FIG. 11. *Anadara perlabiata*, × 2.

PLATE XV

FIG. 1. *Trisodos tortuosa*, ventral view of heart, reconstruction.
FIG. 2. *Arcopsis adamsi*, ventral view of heart and sub-intestinal loop; a reconstruction.
FIG. 3. *Anadara perlabiata*, dorsal view of heart and aortae, a reconstruction.
FIG. 4. *Anadara perlabiata*, cross section of oesophagus.
FIG. 5. *Anadara transversa*, lateral view of digestive system.
FIG. 6. *Barbatia barbata*, intestine and right half of stomach, × 5.
FIG. 7. *Anadara chemnitzi*, intestine and right half of stomach.
FIG. 8. *Anadara perlabiata*, section through palp.
FIG. 9. *Barbatia reticulata*, diagram of kidney and connections; *e*, external opening; *p*, reno-pericardial canal; *r*, opening of kidney into common chamber with gonoduct; *s*, gonad and gonoduct. Ventral view.
FIG. 10. *Cucullaea granulosa*, ventral view of heart; *i*, intestine.
FIG. 11. *Anadara chemnitzi*, abdominal sense organs, × 8.
FIG. 12. *Barbatia barbata*, left half of stomach, × 5.
Fig. 13. *Barbatia gradata*, right half of stomach, × 10.

Plate XVI

Fig. 1. *Anadara incongrua*, intestine and right half of stomach, × 3.
Fig. 2. *Anadara incongrua*, actual length, 60 mm.
Fig. 3. *Anadara incongrua*, main muscles of visceral cavity, × 3.
Fig. 4. *Cucullaea granulosa*, actual length, 70 mm.
Fig. 5. *Cunearca incongrua*, liver follicles and capillary net; connective tissue omitted.
Fig. 6. *Anadara chemnitzi*, main muscles of visceral cavity, × 3.

Plate XVII

Fig. 1. *Anadara perlabiata*, main muscles of visceral cavity, × 3.
Fig. 2. *Anadara chemnitzi*, dorsal view, × 2.
Fig. 3. *Anadara incongrua*, abdominal sense organs.
Fig. 4. *Barbatia barbata*, main muscles of visceral cavity, × 6.
Fig. 5. *Anadara chemnitzi*, × 2.
Fig. 6. *Barbatia gradata*, left half of stomach, × 10.
Fig. 7. *Noetia ponderosa*, × 2. Anterior end below.
Fig. 8. *Argina pexata*, left half of stomach, × 3.
Fig. 9. *Anadara incongrua*, left half of stomach.
Fig. 10. *Cucullaea granulosa*, section through byssus cavity at level of line *a*, Pl. XIX, Fig. 5, × 5.
Fig. 11. *Noetia ponderosa*, right half of digestive system, × 5. Reversed with reference to Pl. XVIII, Fig. 2.

Plate XVIII

Fig. 1. *Noetia ponderosa*, length, 63 mm.
Fig. 2. *Noetia ponderosa*, left half of digestive system, × 5. Reversed with reference to Fig. 11, Pl. XVII.
Fig. 3. *Argina pexata*, × 1.5.
Fig. 4. *Argina pexata*, intestine and right half of stomach, × 3.
Fig. 5. *Argina pexata*, anal region, × 3.
Fig. 6. *Argina pexata*, main muscles of visceral cavity, *p*, pericardium, × 3.

Plate XIX

Fig. 1. *Argina pexata*, heart, dorsal view, × 2.
Fig. 2. *Noetia ponderosa*, abdominal sense organs, × 5.
Fig. 3. *Argina pexata*, intestine, left face.
Fig. 4. *Cucullaea granulosa*, dorsal view of heart, × 5.
Fig. 5. *Cucullaea granulosa*, lateral view of byssus cavity, × 2.
Fig. 6. *Cucullaea granulosa*, right half of stomach, *a*, line of section, Pl. XVII, Fig. 10; arrow points anteriorly, × 4.
Fig. 7. *Glycymeris longior*, intestine and right half of stomach; shell length, 27 mm.
Fig. 8. *Glycymeris subobsoleta*, intestine and right half of stomach.
Fig. 9. *Glycymeris migueliana*, digestive system, left face; length of shell 17 mm.

Plate XX

Fig. 1. *Glycymeris americana*, lateral view of digestive system.
Fig. 2. *Barbatia reticulata*, mantle epithelium, outer surface to left.
Fig. 3. *Glycymeris longior*, muscles of visceral cavity, × 3.
Fig. 4. *Glycymeris longior*, × 5.
Fig. 5. *Glycymeris longior*, ventral view of anal region, × 6.
Fig. 6. *Glycymeris americana*, left half of stomach.
Fig. 7. *Glycymeris longior*, × 2.5.
Fig. 8. *Glycymeris migueliana*, right half of stomach, × 10.
Fig. 9. *Cucullaea granulosa*, anal region, × 4.

FIG. 10. *Glycymeris migueliana*, anal region, × 4.
FIG. 11. *Glycymeris migueliana*, left half of stomach, × 10.
FIG. 12. *Cucullaea granulosa*, muscles of visceral cavity, × 2.

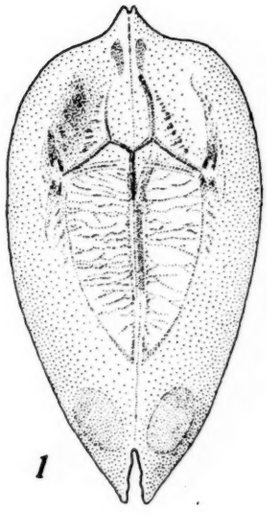
PLATE XXI

FIG. 1. *Glycymeris americana*, × 1.
FIG. 2. *Glycymeris subobsoleta*, main muscles of visceral cavity slanted for sake of clearness, × 6.
FIG. 3. *Glycymeris americana*, main muscles of visceral cavity; *p*, pericardial cavity, × 2.
FIG. 4. *Glycymeris subobsoleta*, lateral view of stomach with attached muscles and bile ducts (*b*), × 2.
FIG. 5. *Glycymeris americana*, intestine and right half of stomach.
FIG. 6. *Glycymeris americana*, abdominal sense organs, × 4.
FIG. 7. *Glycymeris longior*, left half of stomach.
FIG. 8. *Cucullaea granulosa*, lateral view of digestive system, × 2
FIG. 9. *Noetia ponderosa*, muscles of visceral cavity, × 3.

PLATE XXII

FIG. 1. *Arca imbricata*. Lateral view of right half of anterior end of body, × 6.
FIG. 2. Cross section of stomach of *Acar gradata*.
FIG. 3. Cross section of stomach of *Acar pernoides* at about the same level as Fig. 2.
FIG. 4. Anal region of *Arca imbricata*, × 5.
FIG. 5. Reconstruction of circumesophageal nerve ring of *Acar pernoides*.
FIG. 6. Reconstruction of digestive system of *Acar pernoides* viewed from left side; *a*, *b* lines corresponding respectively to Figs. 9, 10 on this plate.
FIG. 7. Reconstruction of digestive system of *Acar gradata* viewed from left side.
FIG. 8. Cross section of the most dorsal pair of esophageal glands.
FIG. 9. Cross section of *Acar pernoides* through most ventral pair of esophageal glands and cerebral ganglia; along line *a*, Fig. 6.
FIG. 10. Cross section of *Acar pernoides* through most dorsal pair of esophageal glands and pedal ganglia; along line *b*, Fig. 6.

PLATE I



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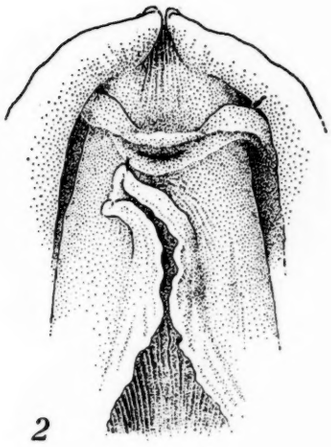

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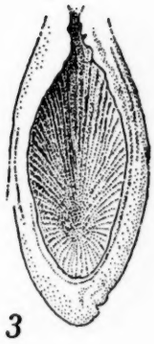

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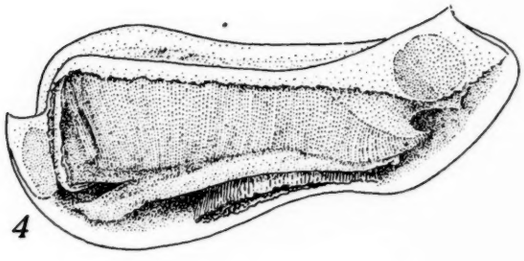

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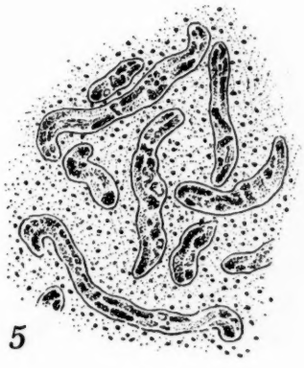

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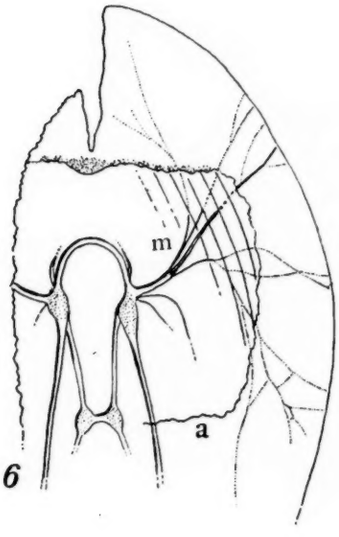

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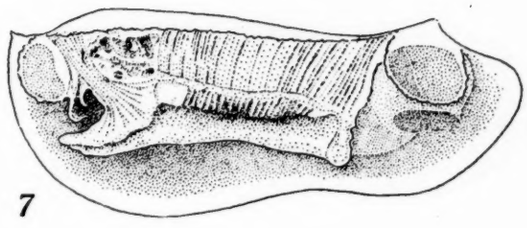

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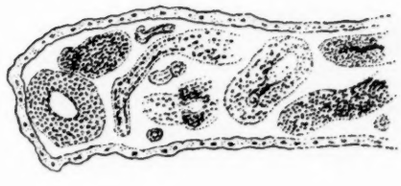

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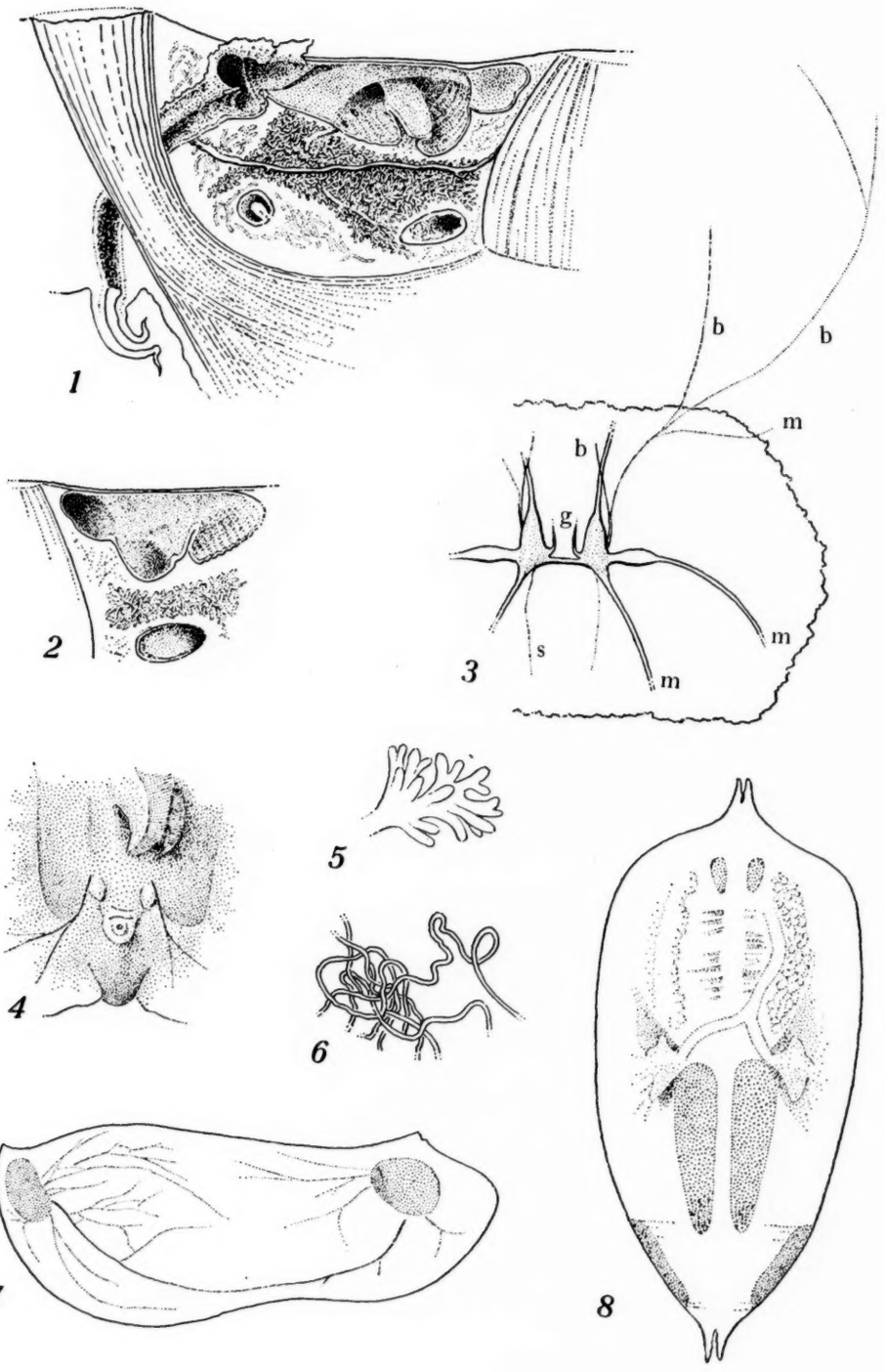
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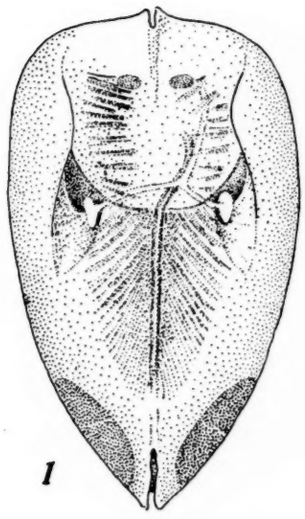

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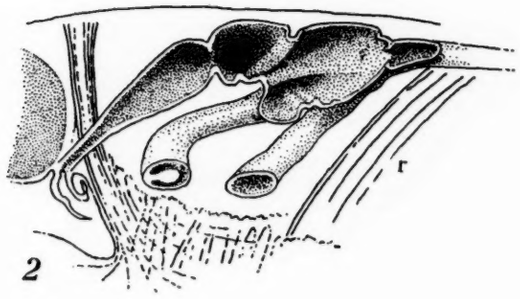

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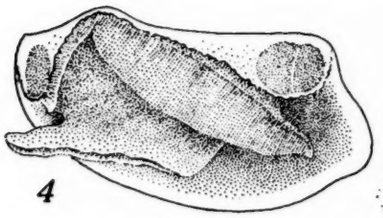

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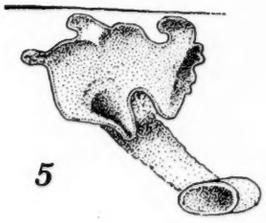

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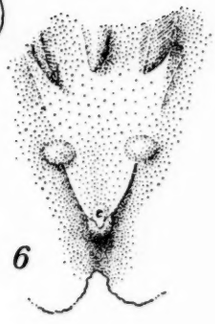

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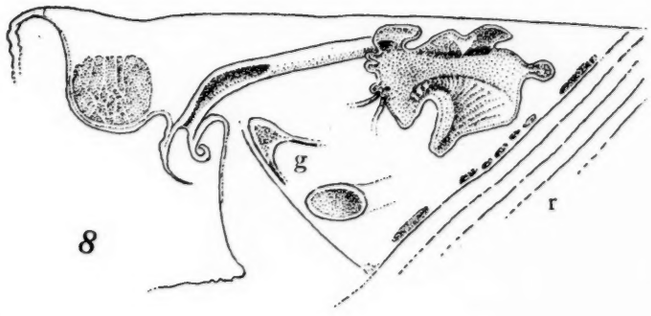

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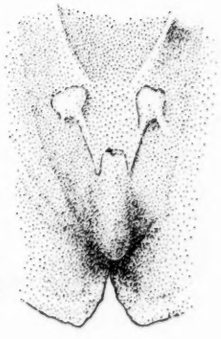

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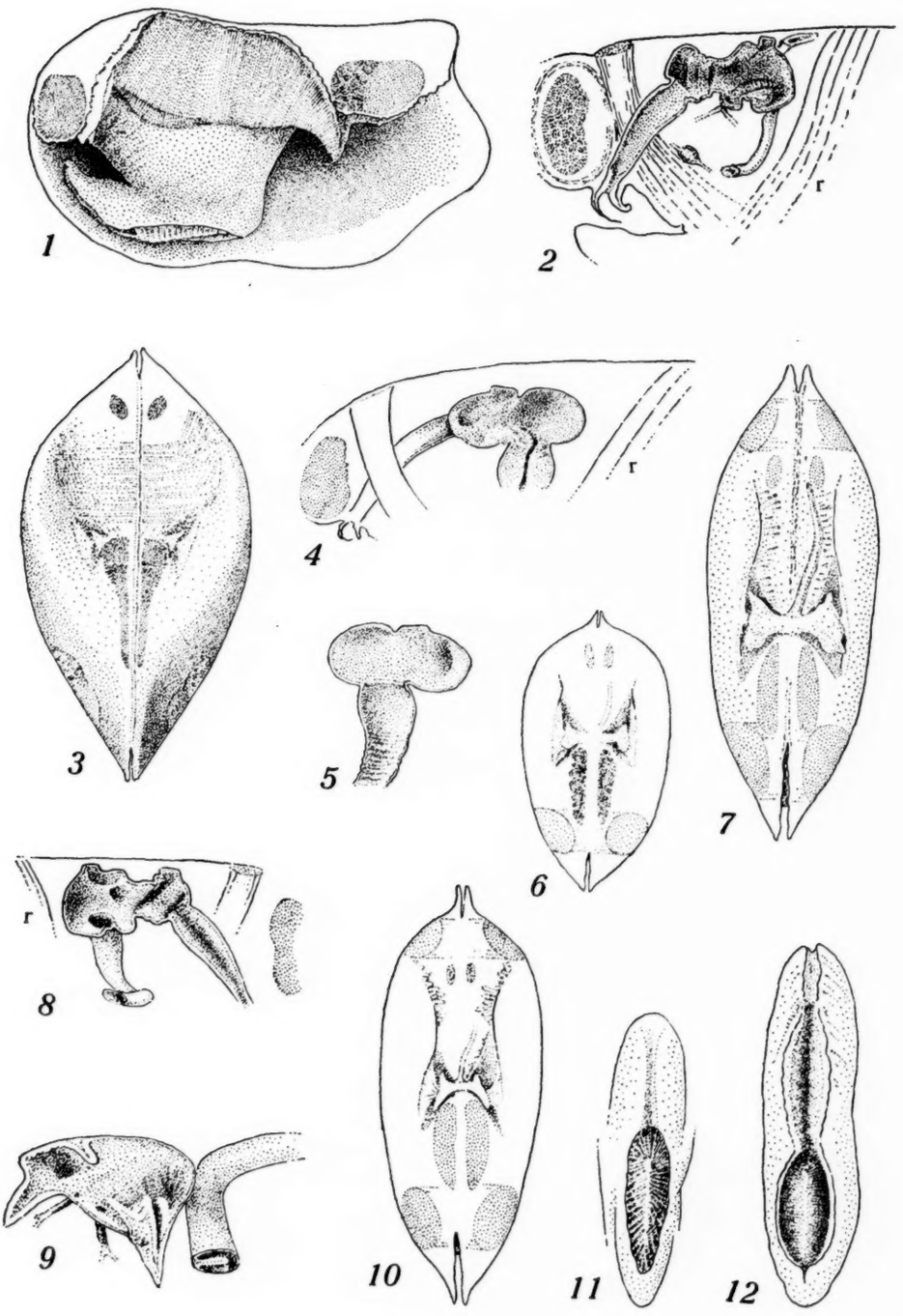
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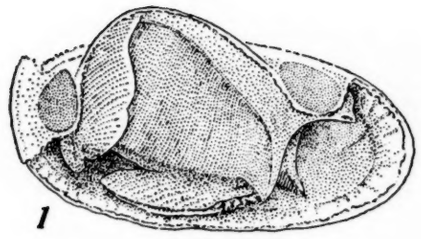

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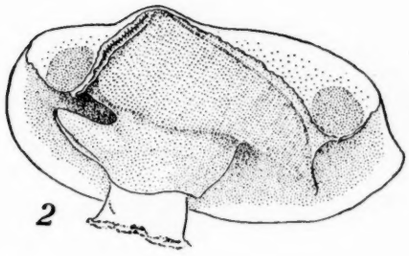

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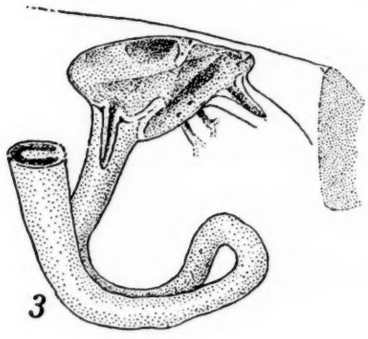

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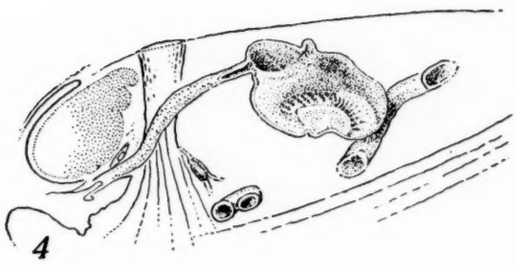

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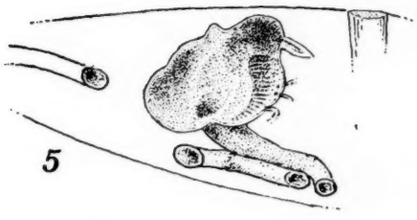

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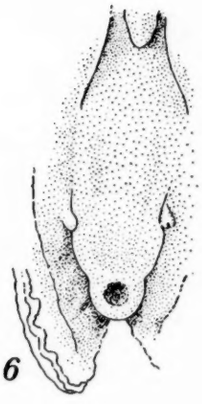

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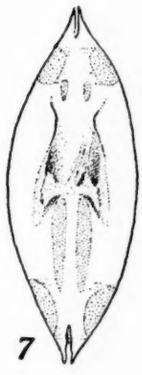

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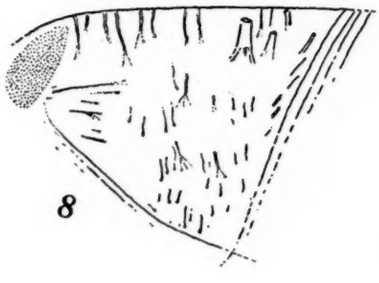

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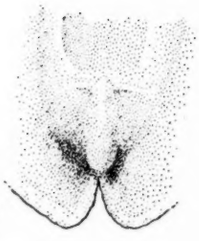

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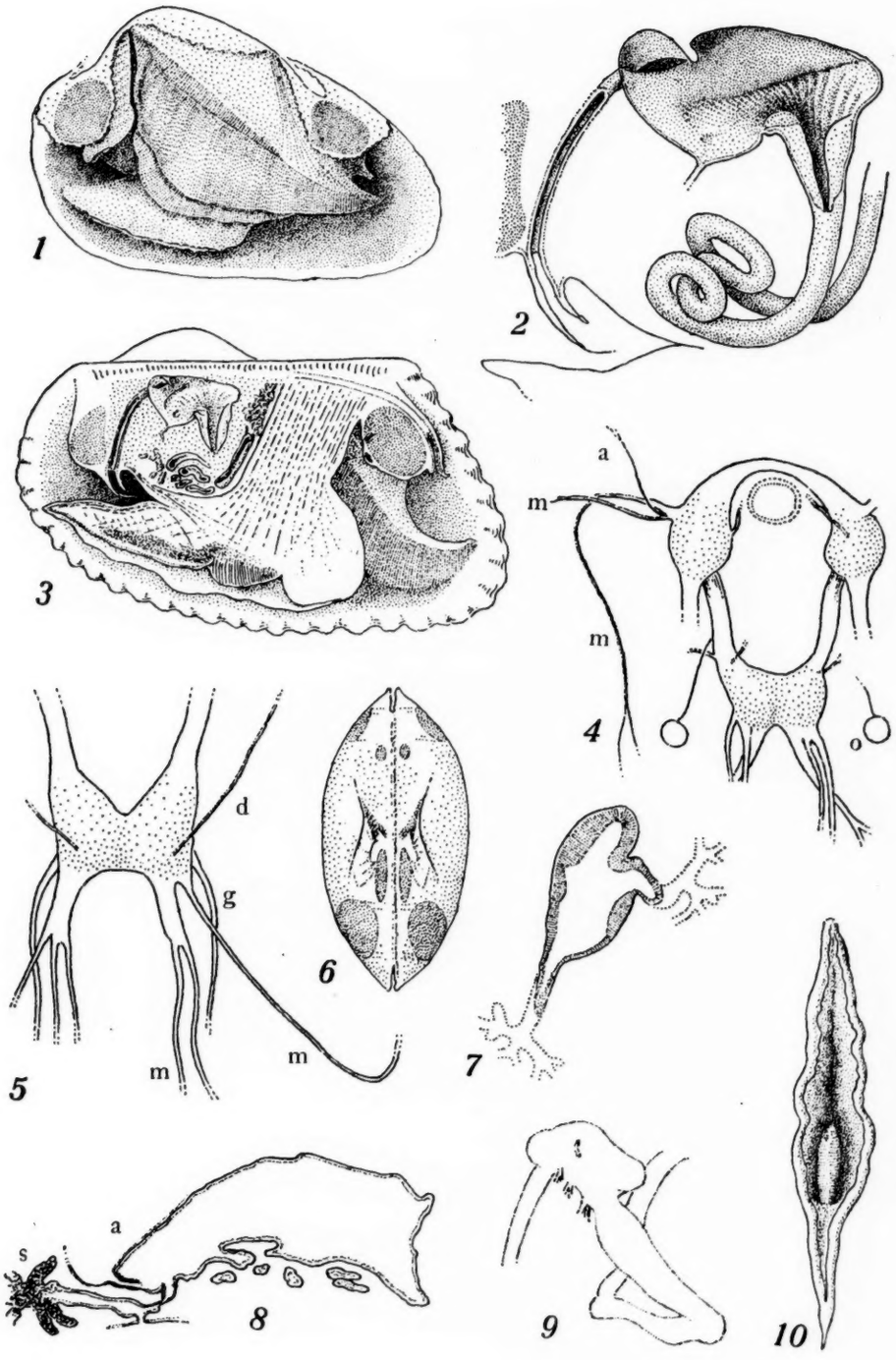
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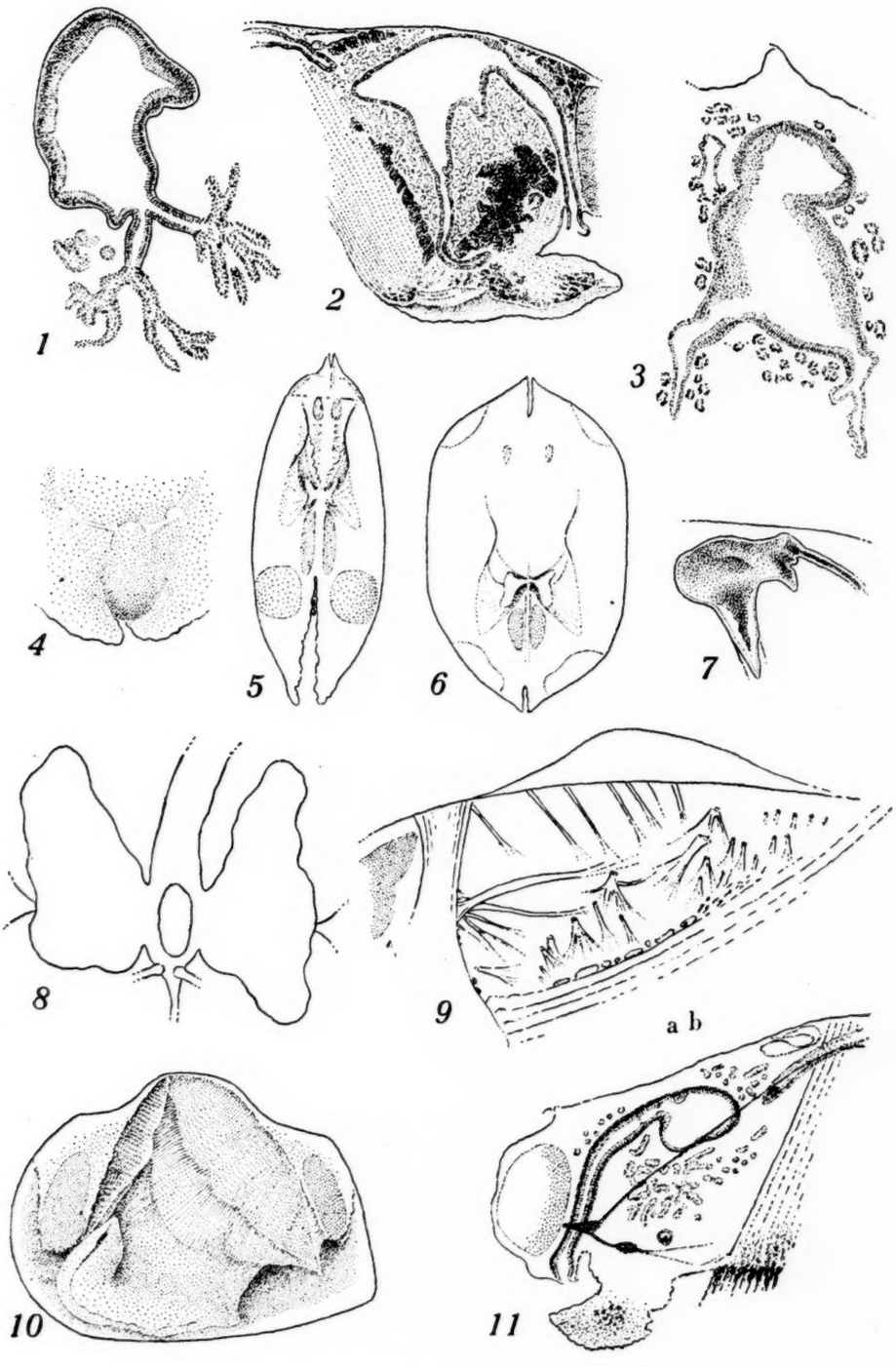
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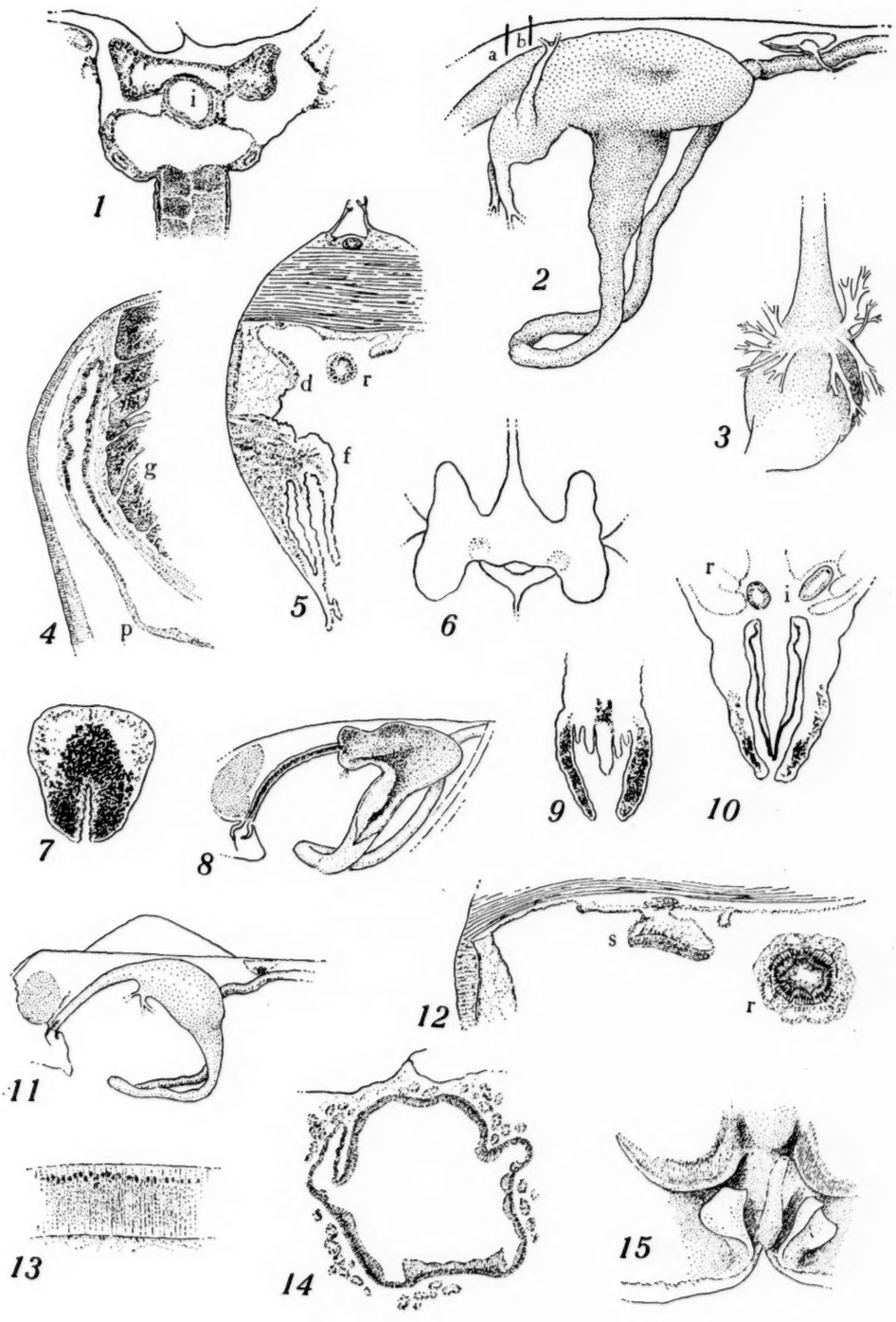
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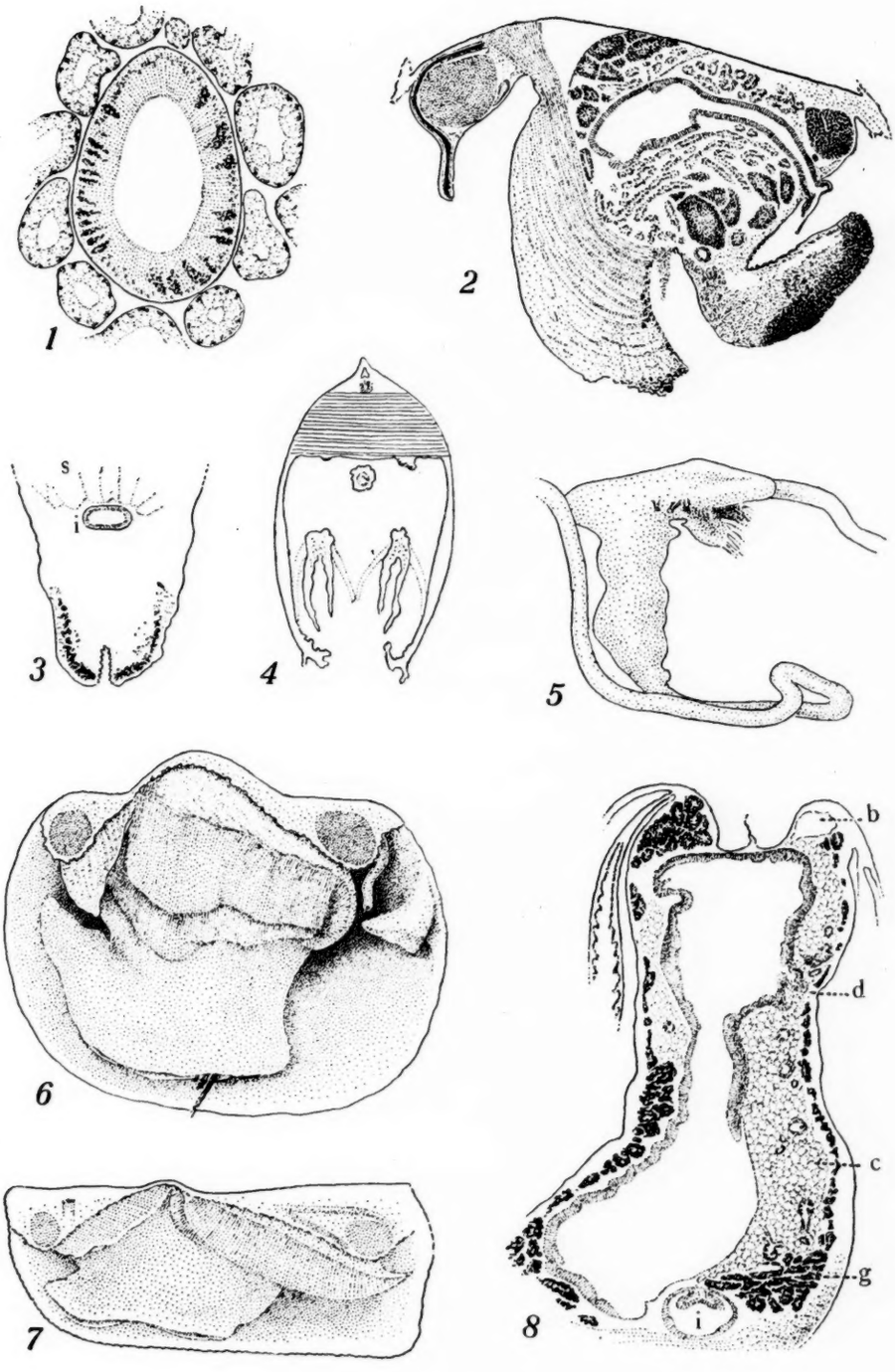
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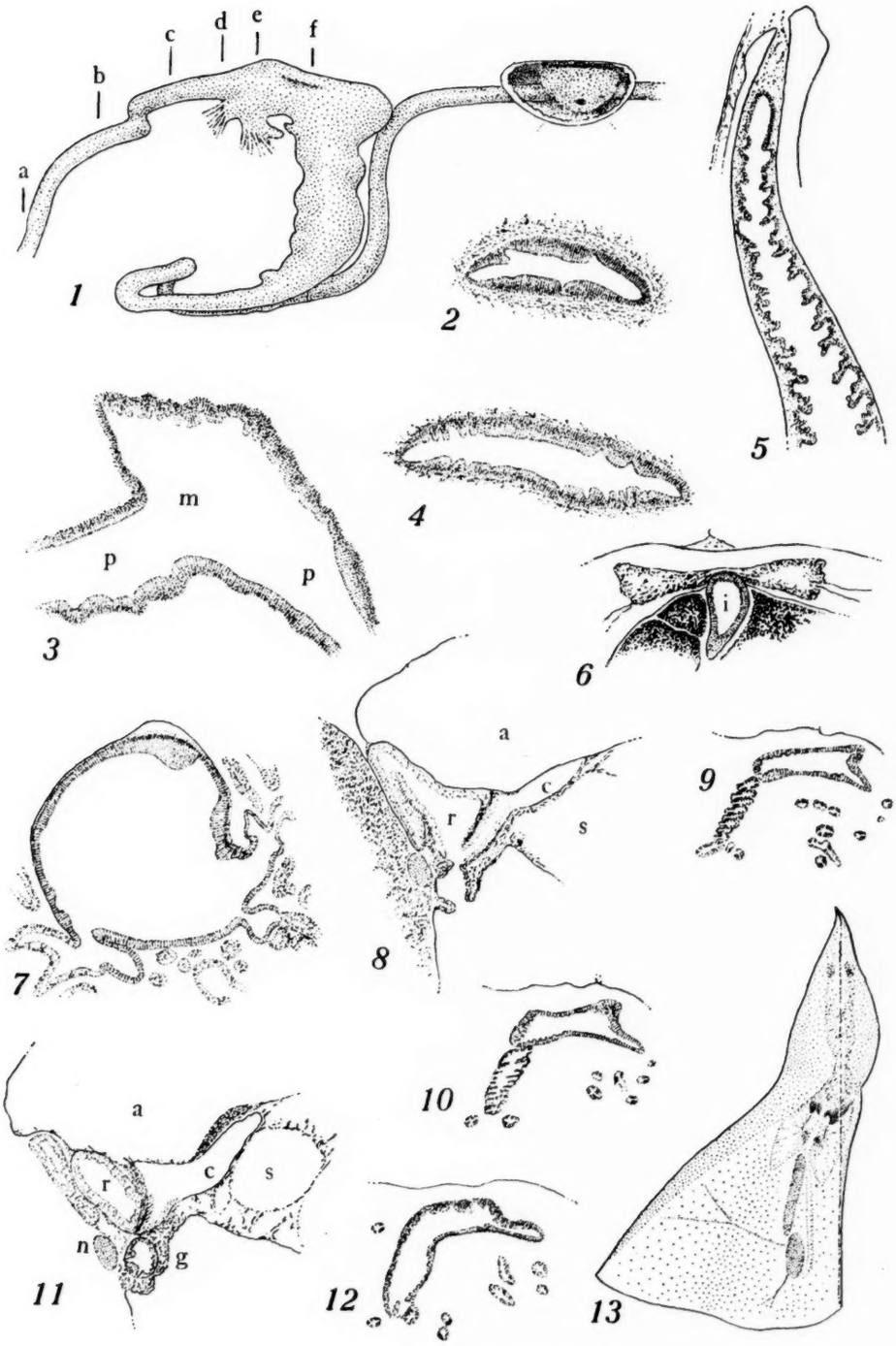

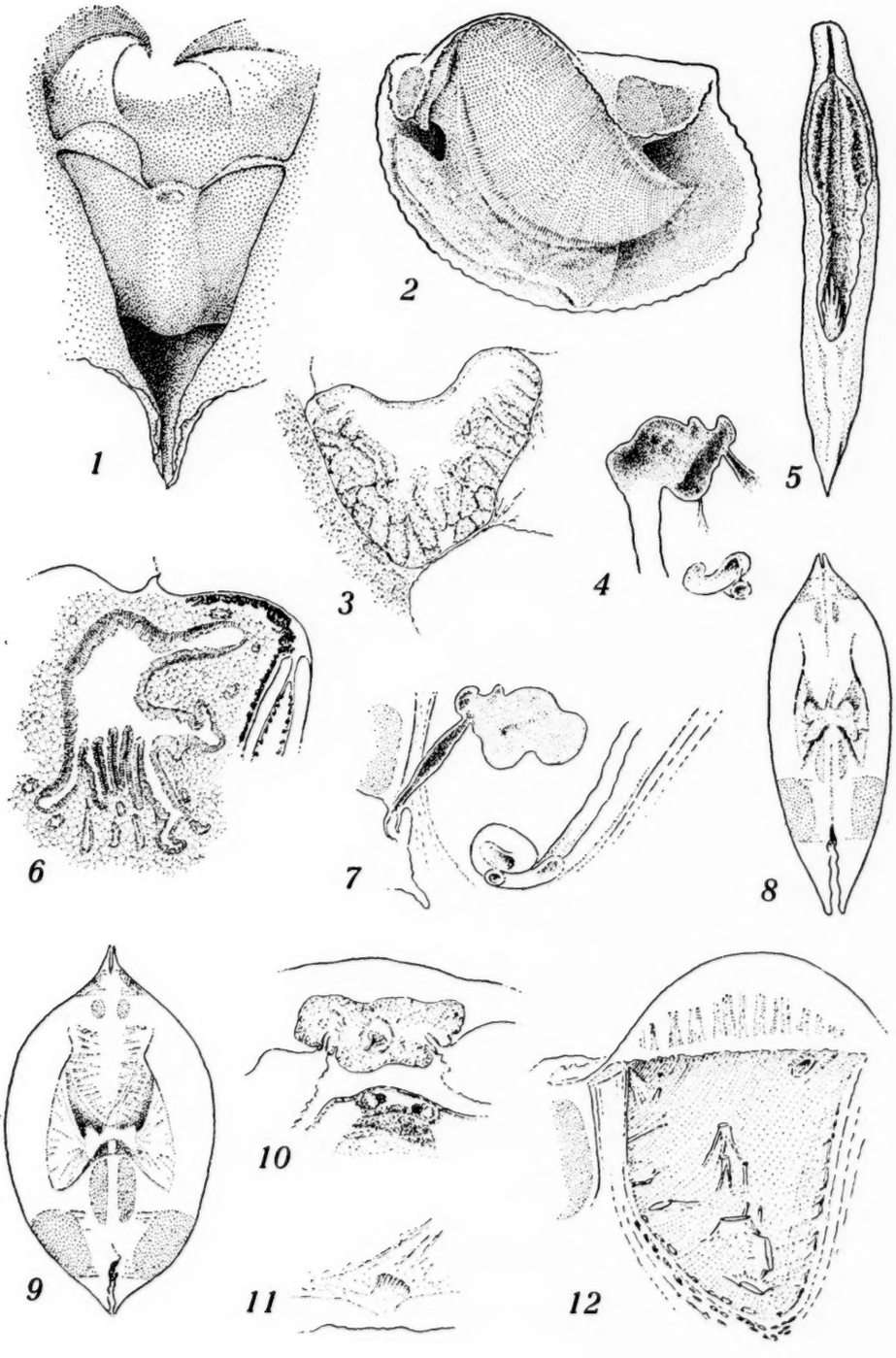
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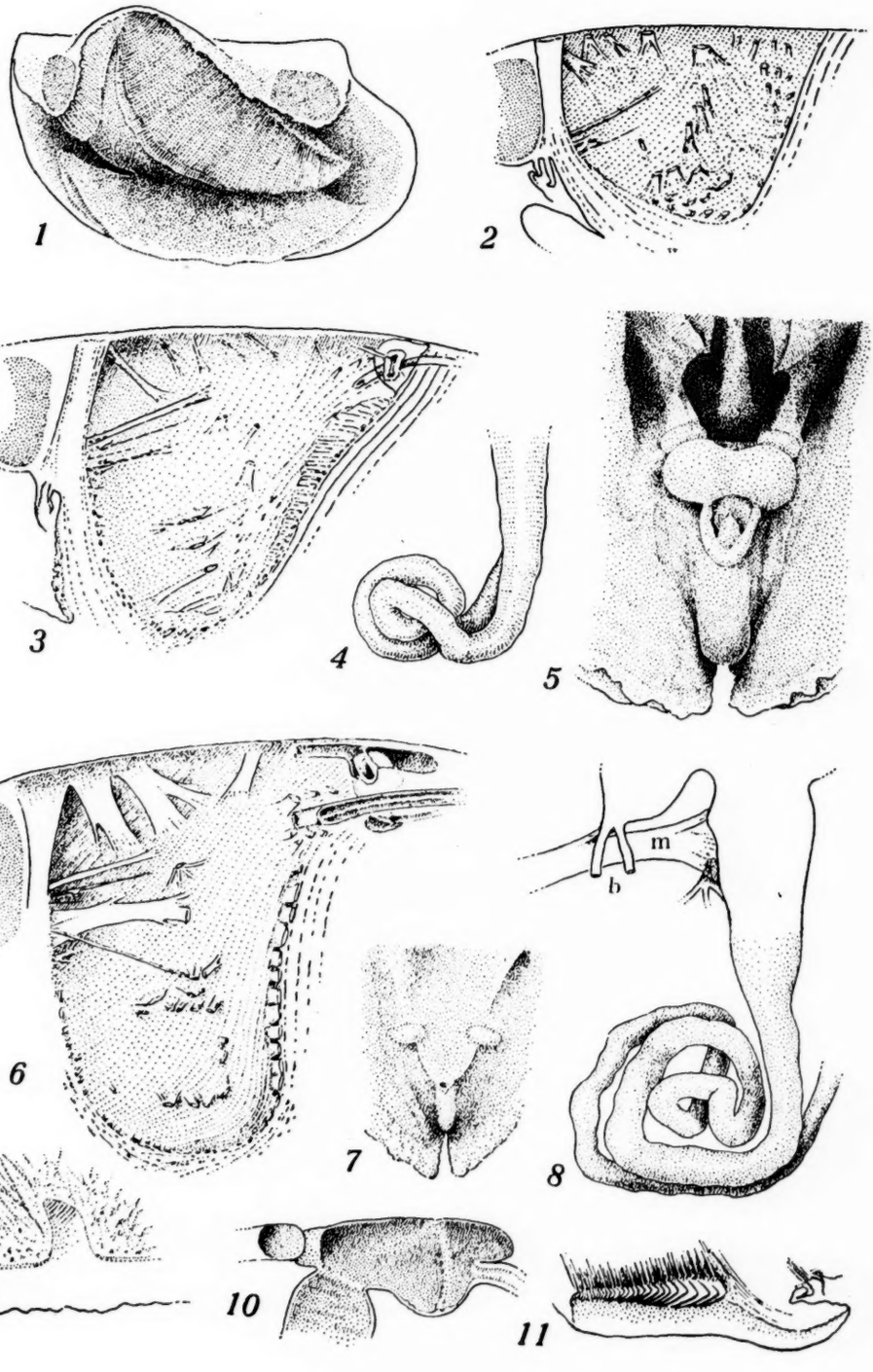
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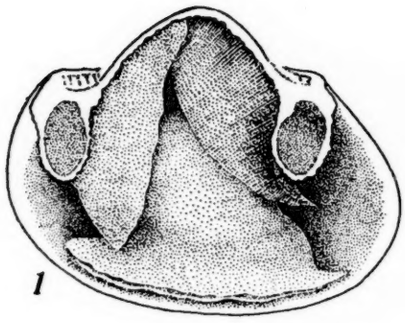

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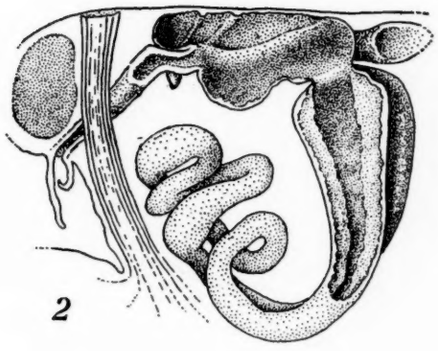

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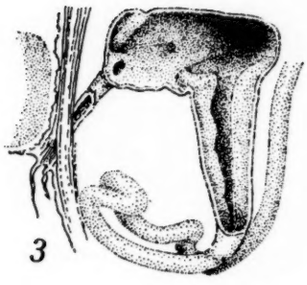

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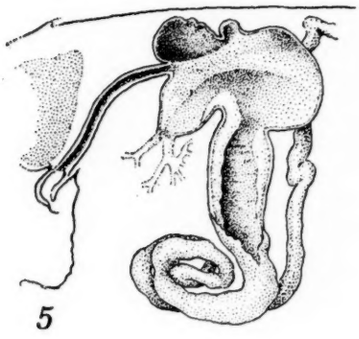

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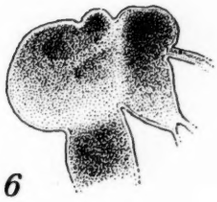

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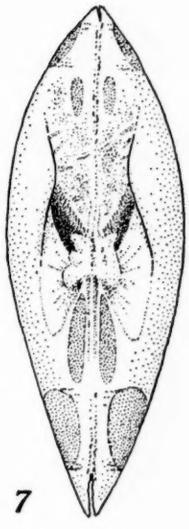

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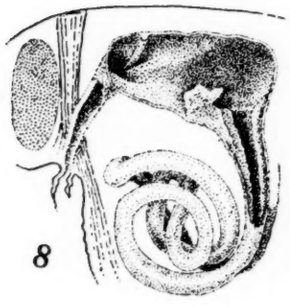

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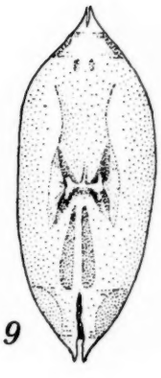

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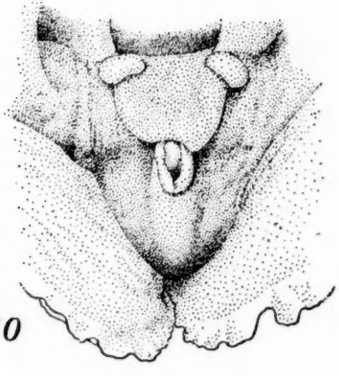

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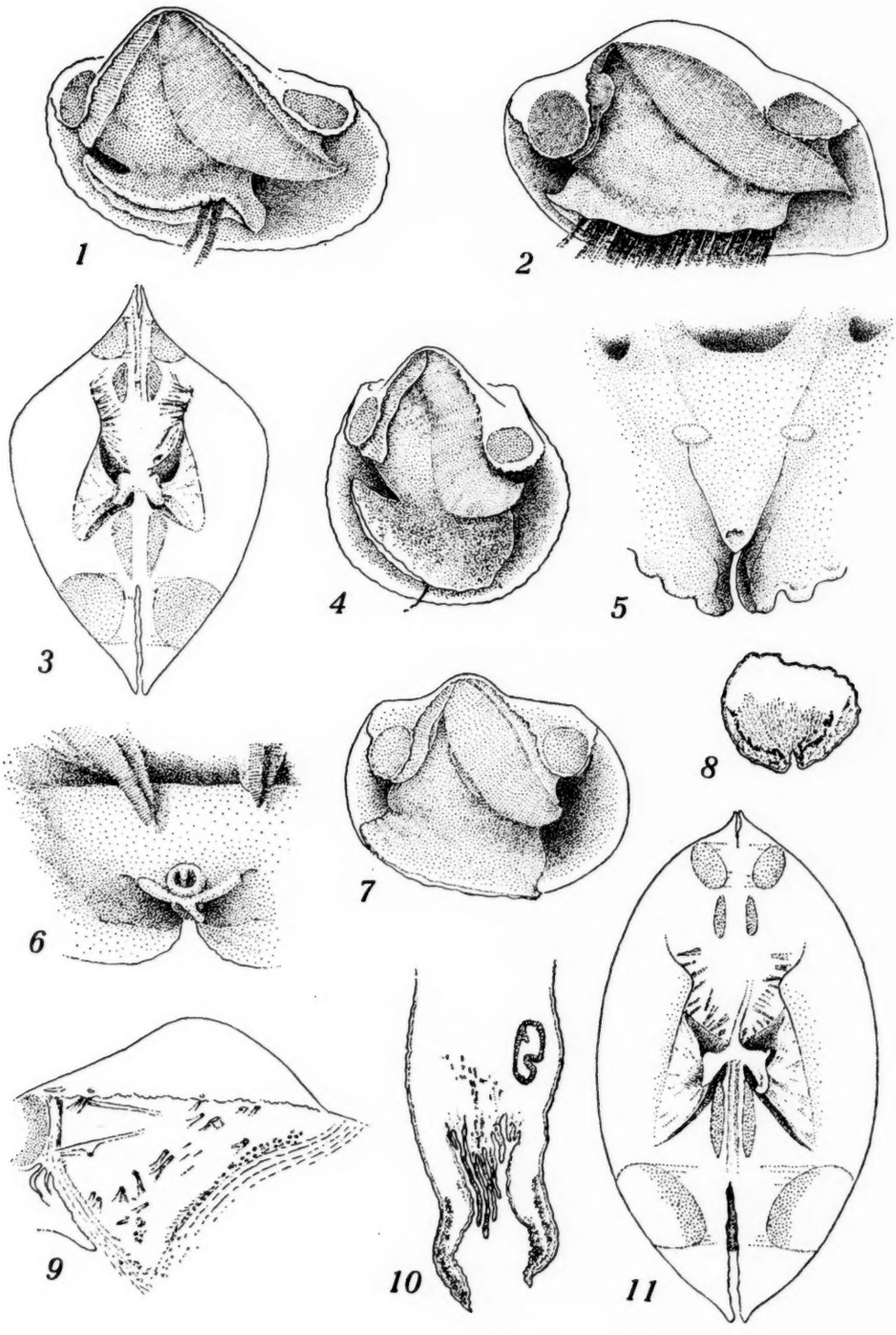
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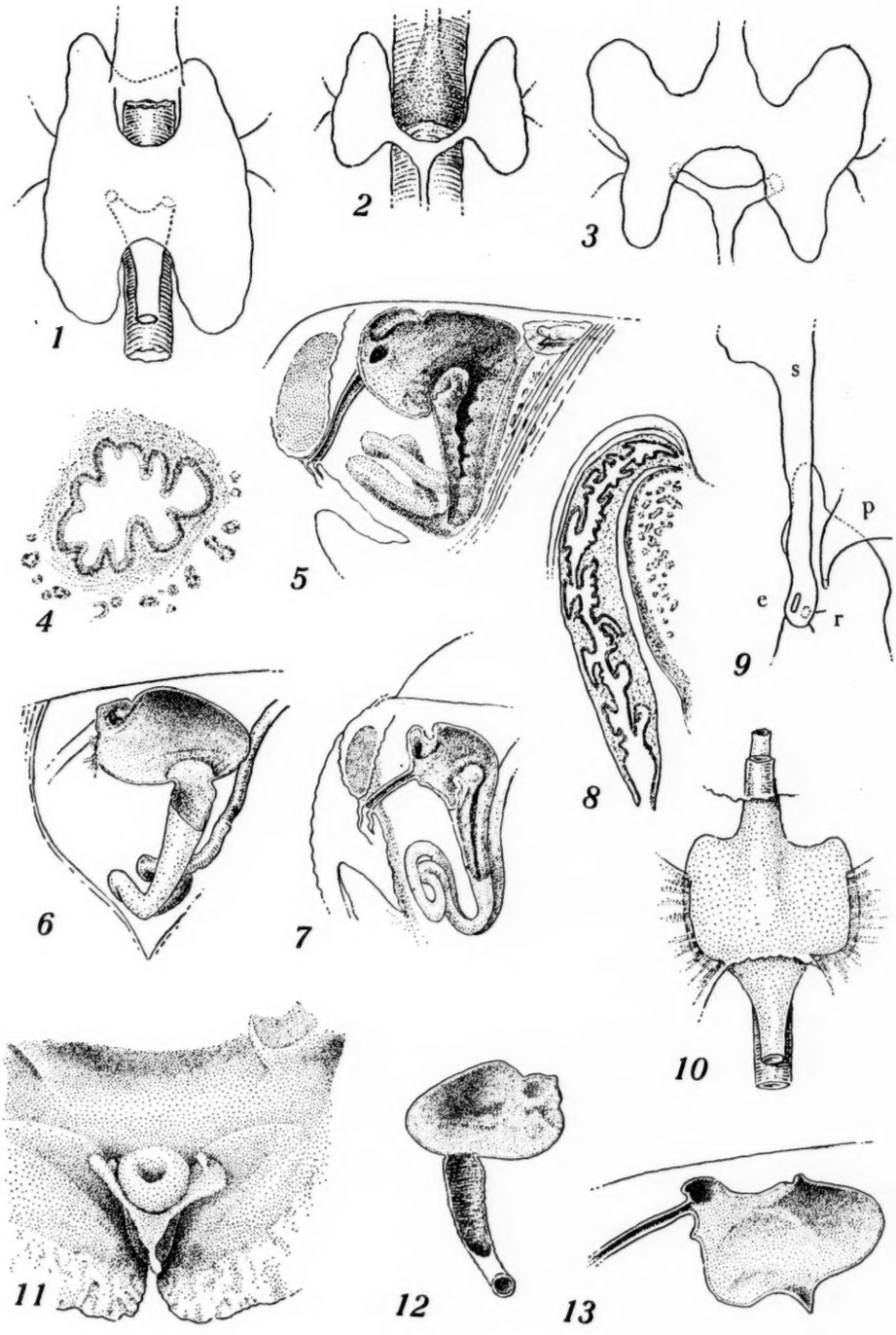
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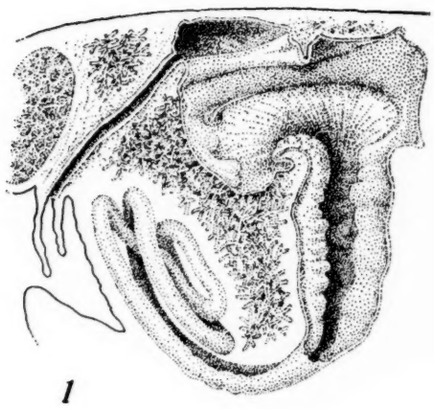

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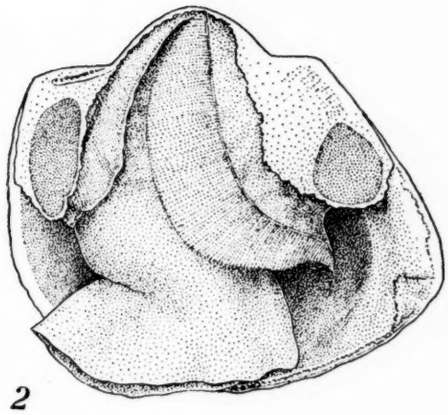

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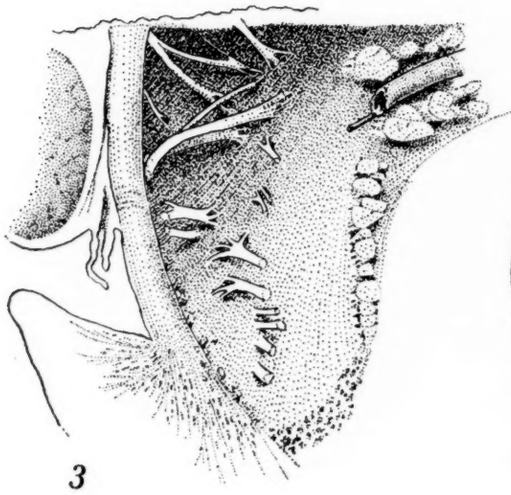

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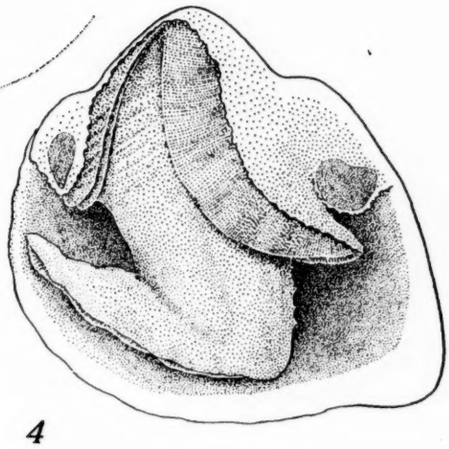

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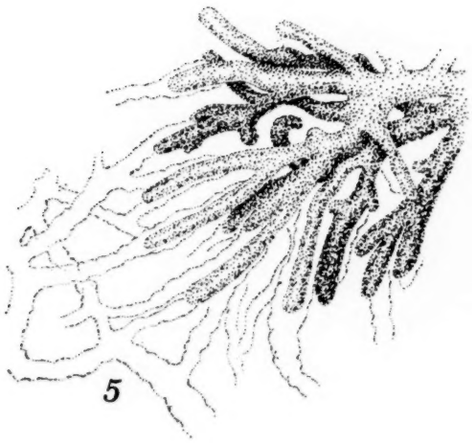

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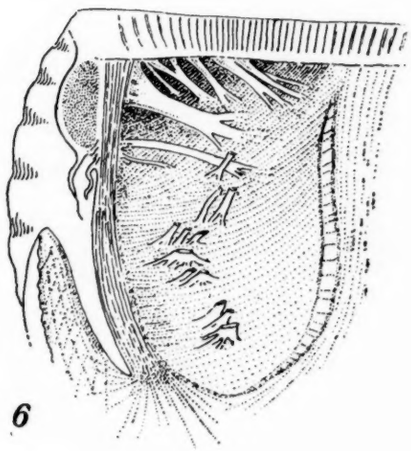

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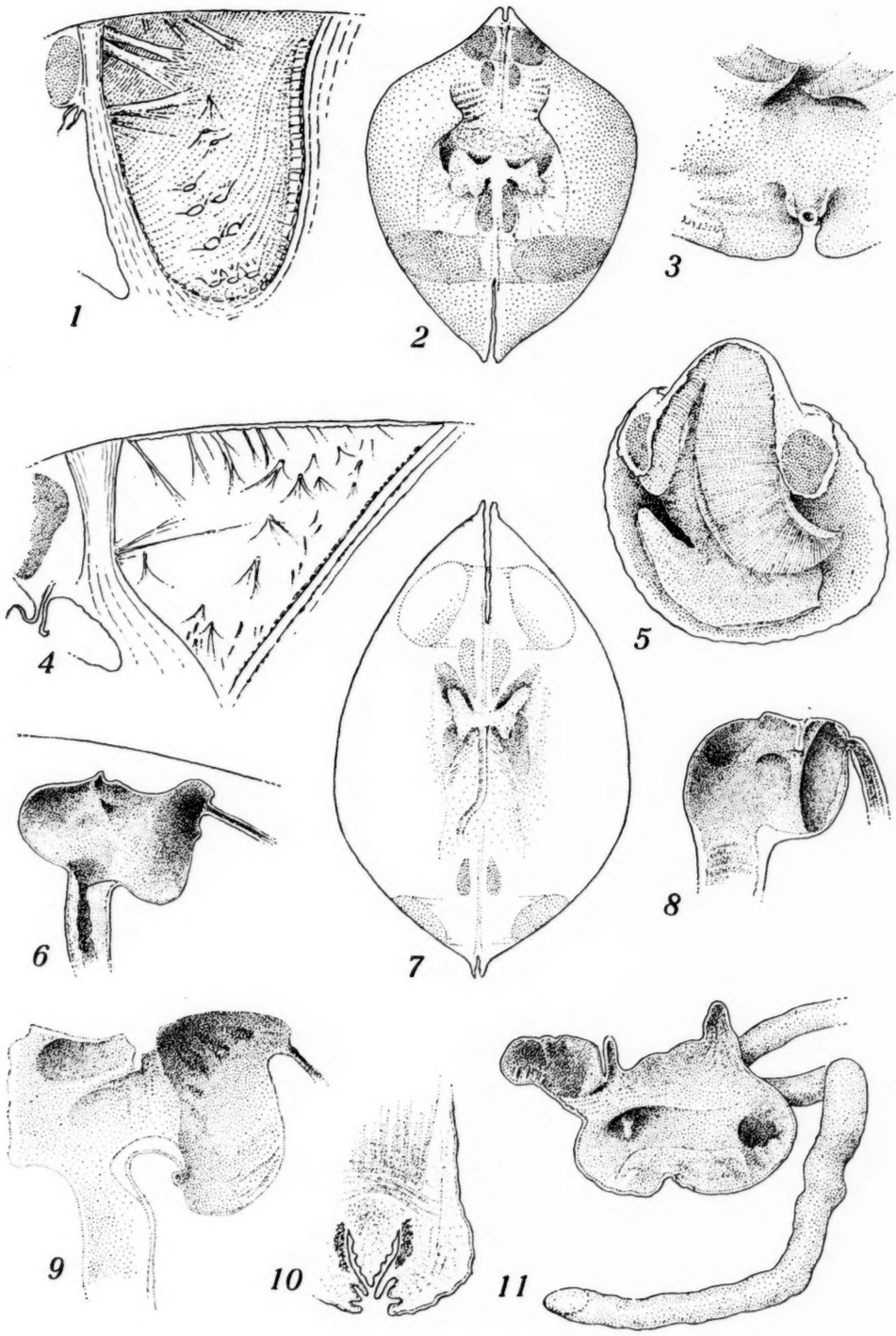

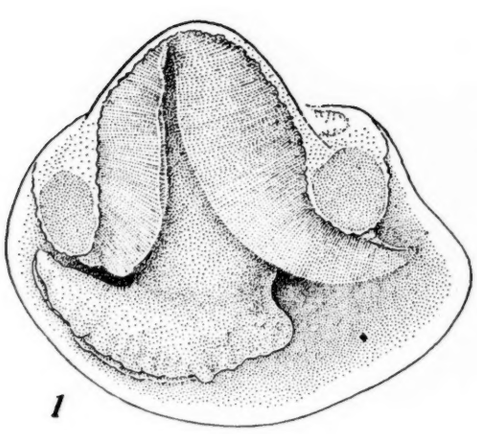

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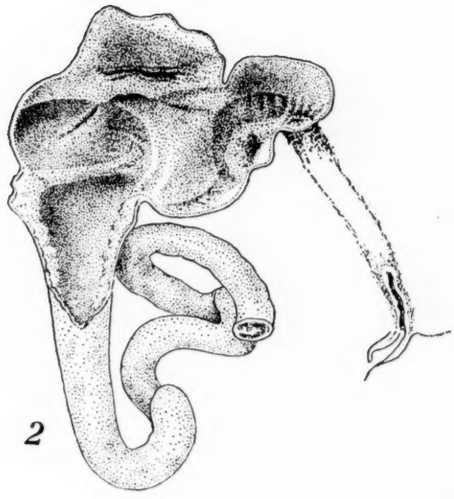

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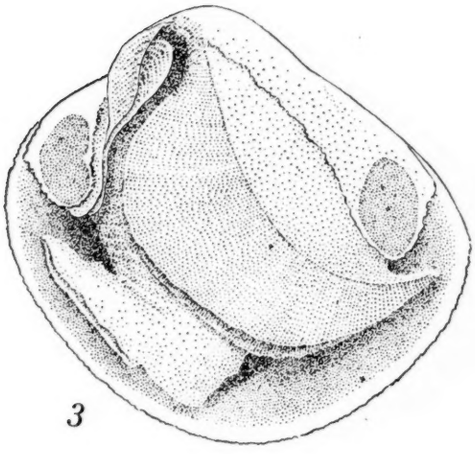

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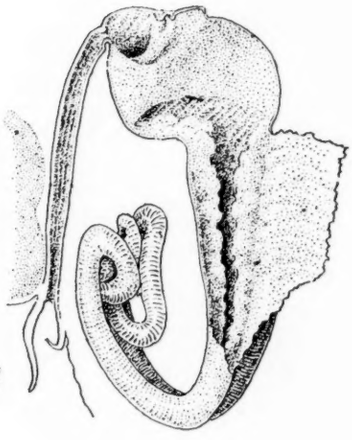

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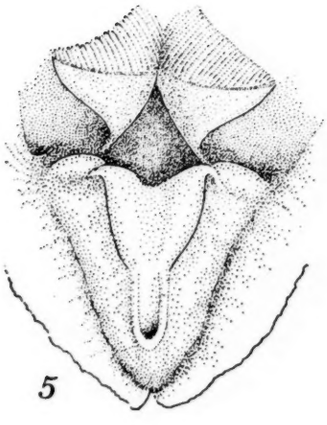

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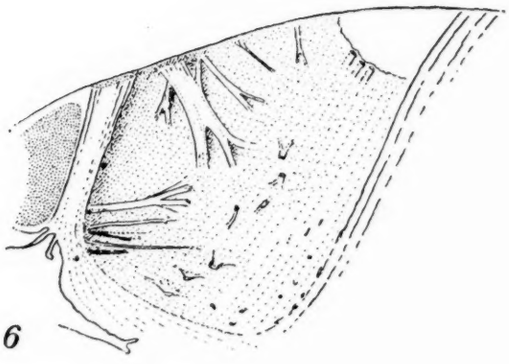

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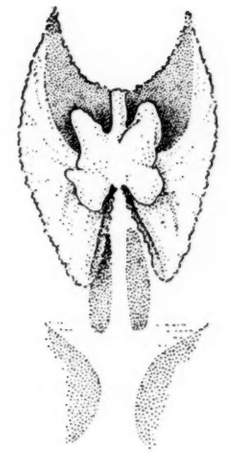

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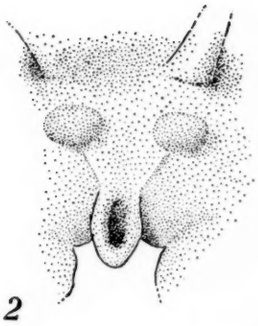

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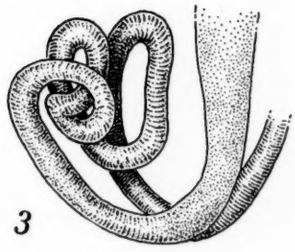

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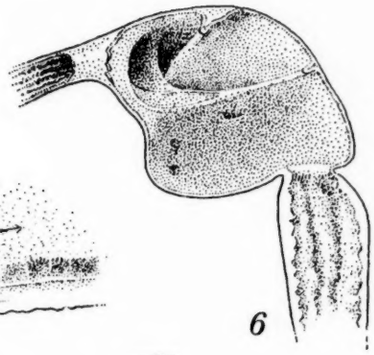

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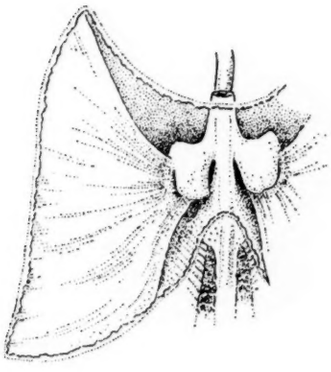

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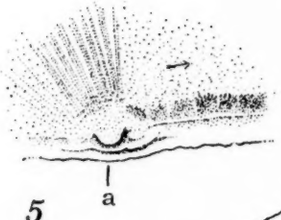

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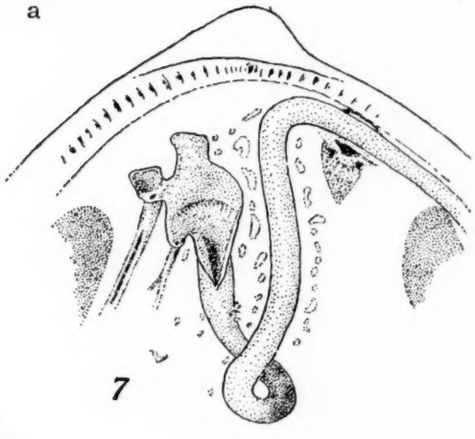

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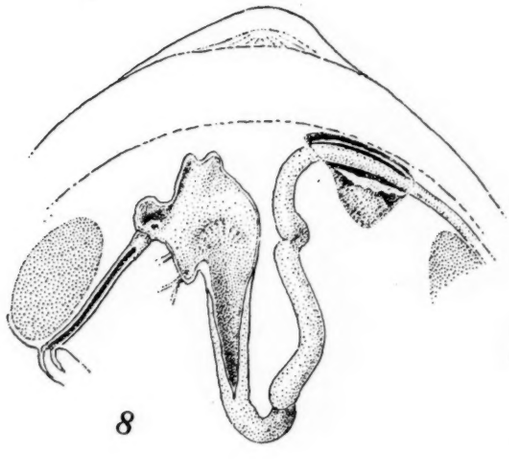

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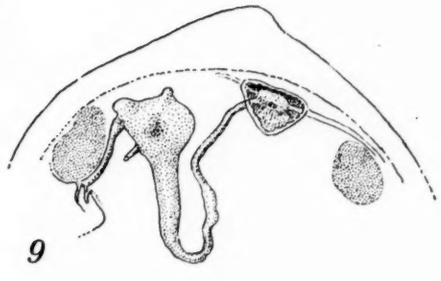

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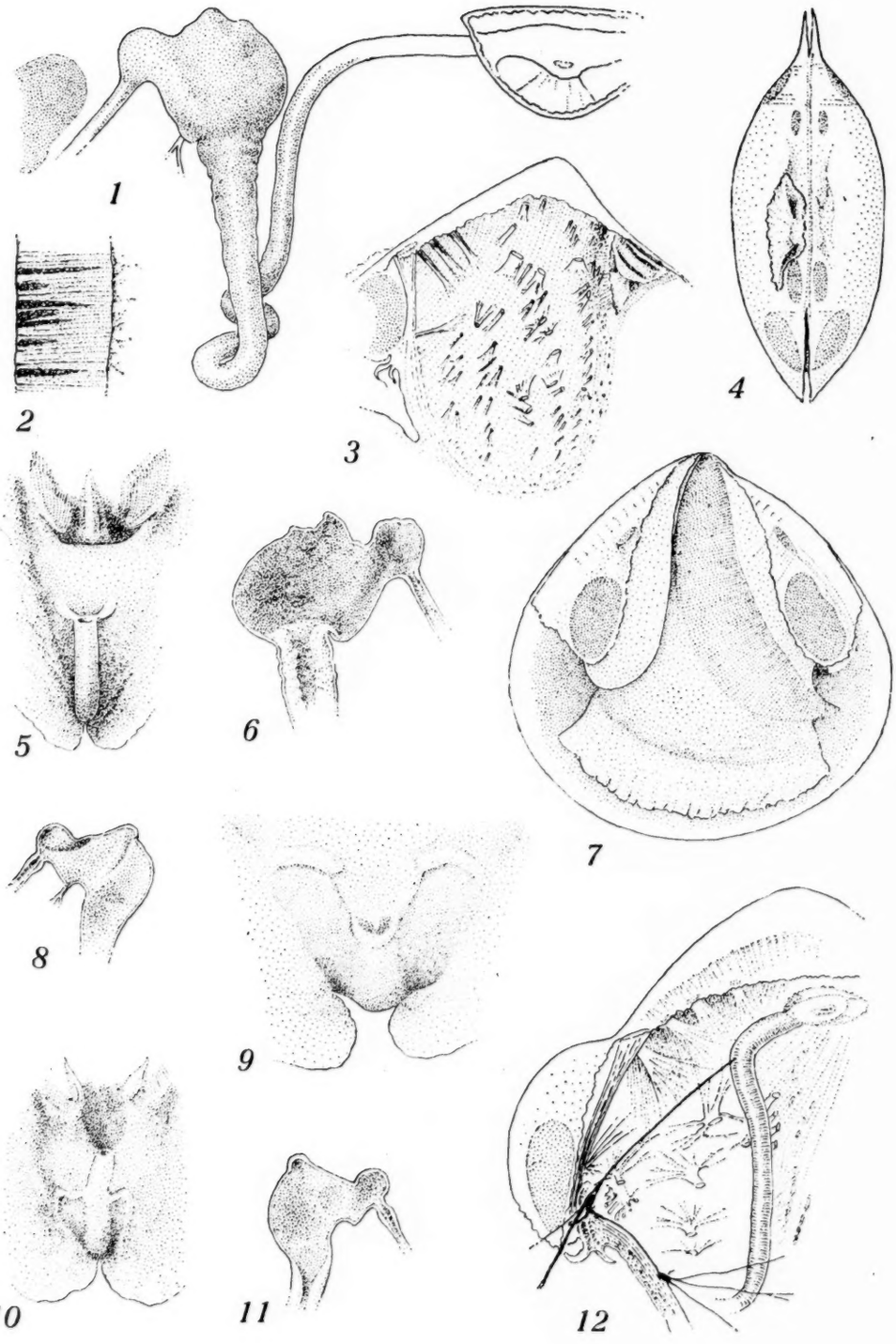
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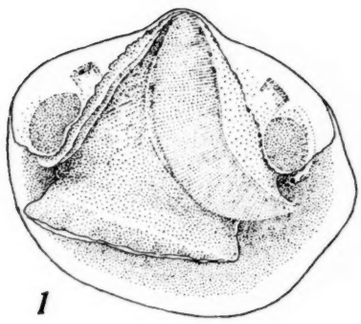
PLATE XXI



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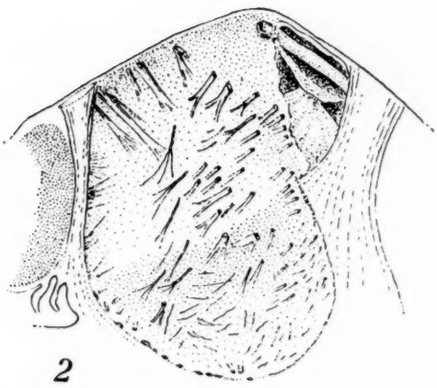

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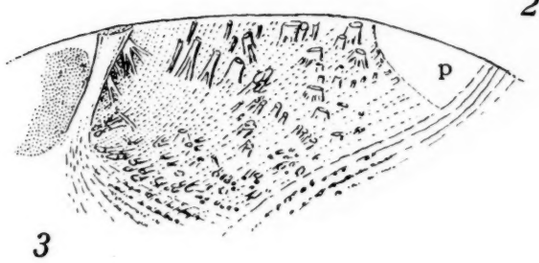

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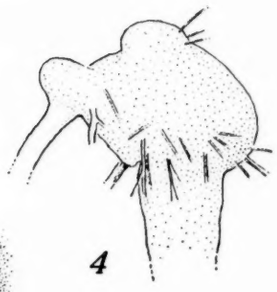

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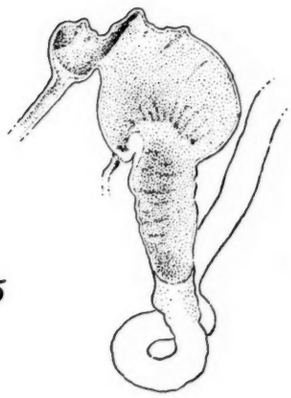

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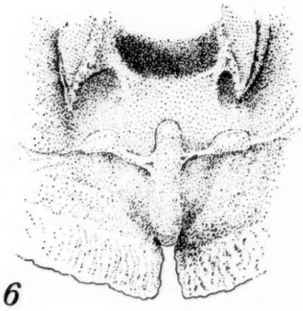

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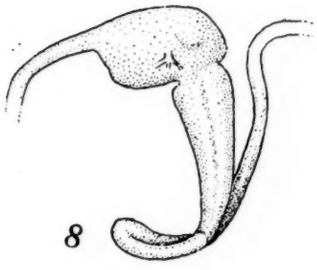

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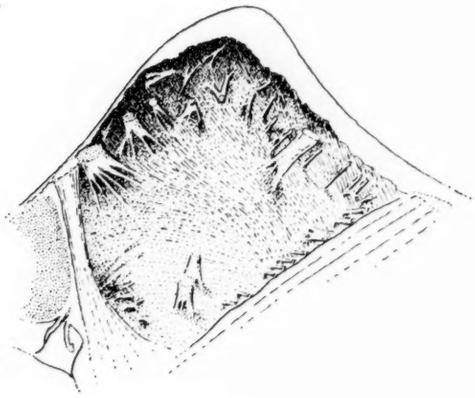

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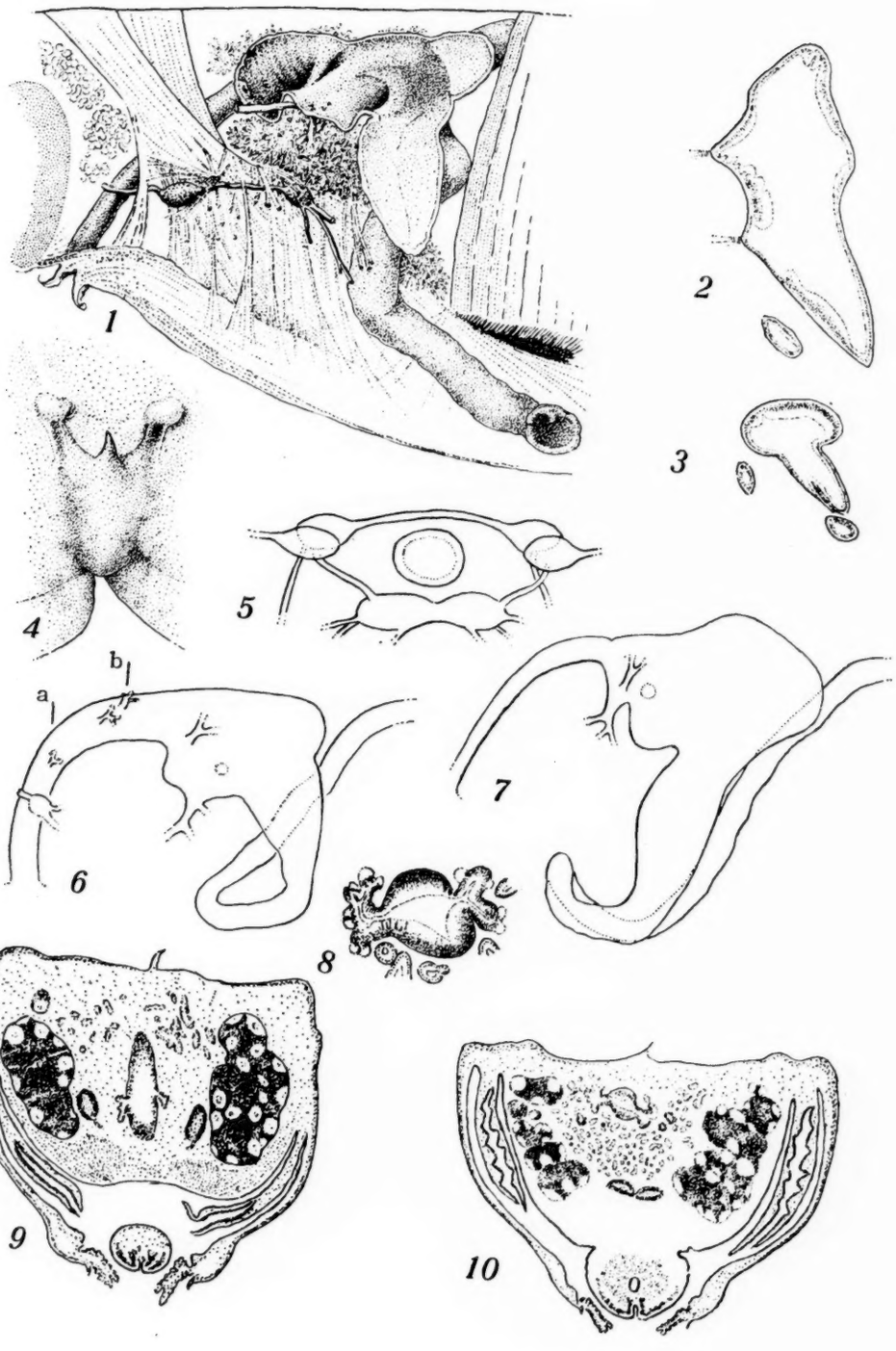

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AUGUST, 1941

THE BRAIN AND ITS RÔLE IN THE PHYLOGENETIC TRANSFORMATION OF THE HUMAN SKULL

FRANZ WEIDENREICH

Cenozoic Research Laboratory, Peiping
Union Medical College

PHILADELPHIA:

THE AMERICAN PHILOSOPHICAL SOCIETY

104 SOUTH FIFTH STREET

1941

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Cenozoic Research Laboratory, Peiping Union Medical College, Peking, China

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PREFACE

The study presented herein constitutes one year's work carried out at the American Museum of Natural History in New York, while on furlough. It would have been impossible to complete this work without the generous help of the Administration and the Heads of the Department of Comparative Anatomy, Dr. William K. Gregory, Department of Anthropology, Dr. Clark Wissler, and the Department of Palaeontology, Drs. Barnum Brown and Walter Granger, who very kindly arranged for working facilities, placing the personnel of their laboratories, collections, library and every possible assistance at my disposal. Thanks are also due to numerous other colleagues who aided me with advice and suggestions, especially Drs. Edwin H. Colbert, G. Miles Conrad, Raymond M. Gilmore, J. E. Hill, Ernst Mayr, George D. Pinkley, Henry C. Raven, B. Schaeffer, Harry L. Shapiro and G. G. Simpson. I am particularly indebted to Dr. Harold J. Coolidge, Jr., of the Museum of Comparative Zoölogy in Cambridge, who provided important data on the pigmy chimpanzee material, to Mr. Sidney Shapiro who helped me in computing the mathematical formulae, to Mr. Otto Falkenbach of the Laboratory of Palaeontology to whom credit must be given for the extraordinary understanding and technical skill shown in making the reconstruction of the *Pithecanthropus* Skull IV. The excellent drawings illustrating this publication were made by Miss D. F. Levett Bradley. I also wish to express my gratitude to all the librarians of the Museum, especially Miss Jannette M. Lucas who assisted me in finding the necessary literature references. I am especially grateful to Miss Mabel R. Percy who was always ready to help me to overcome the difficulties met with under unfamiliar working conditions, and to Mrs. O. Hempel-Gowen in Peking whose ever untiring efforts prepared this study for publication.

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Introductory

Whenever physical anthropology attempts to trace the line of human evolution by comparing stages of intermediary character with certain types of primates, on one hand, and recent man, on the other, there is no more promising way than the use of the general methods of comparative anatomy which consist (1) in defining all the specific structures of the body and (2) in determining type and degree of their subsequent changes experienced in the course of time. The reliability of this method is reputed to be proved beyond any serious objection by its successfully having exposed the fundamental relations and differences existing between the various groups and types of the animal kingdom.

It is evident that in so doing morphology must play the major rôle whereas problems involving the special significance of features must be ranged secondarily. But even in such cases where an understanding of the form can be obtained only by revealing the direct cause of its shaping, the studies usually are restricted to the closest local relations without any special consideration of further connections.

A typical example of the shortsightedness of such a point of view is presented by the theory on the origin of the human chin, once advocated by the German dentist Walkhoff. The simple fact that skiagrams of the human chin show triangular blackening of the spongy substance, entirely absent in the corresponding region of anthropoid mandibles, induced that author to the belief that the muscles of the tongue and the hyoid bone which arise from or are inserted into the symphysis of the mandible are able to produce not only special systems of cancelli within the bone itself, but also a bulging of its opposite surface. Moreover, this transformation of the bone structure is taken to be the result of a special reaction brought about by the particular use of those muscles in acquiring the faculty of speech. It is significant that such a claim, though lacking any substantial proof, nevertheless met with some approval at that time. Even today occasional references are made to this theory, despite the evidence to the contrary (cf. Weidenreich, 1934). The formation of the mental process and the chin is not at all a local occurrence but a part of the general transformation of the skull—both cranium and face—during the course of human evolution, while the acquisition of the faculty of speech is only a secondary event.

Likewise untenable is Aichel's (1916/17) idea which considers the formation of the heavy supra-orbitals of great apes and fossil man as a direct reaction of the periosteum of the frontal bone thus responding to stimuli caused by an increased activity of the corrugator supercilii. The disappearance of these structures in modern man should be taken as the consequence of the gradual weakening of this muscle. The supra-orbitals, too, are only parts of a general structure exclusively determined by the special character of the skull. (See below.) More examples of those shortsighted explanations are contained in Gegenbaur's interpretation of the air sinuses as being merely secondary expansions of the olfactory region, or the view, almost generally accepted, that the characteristic alterations of the dentition undergone during the human evolution should be due to changes in diet which are supposed to be chiefly of mechanical nature.

In contrast to those views, I have repeatedly attempted to prove that an accurate knowledge of all those phylogenetic processes can be gained only if the body is considered as a totality, that is to say, as a unique construction in which all parts harmonize from the beginning of its organization and in which every essential alteration must be accounted as a consequence of a change in the entire construction.

For instance, the anatomical structure of the human foot proves that it has evolved from an originally grasping foot adapted to climbing conditions (Weidenreich, 1921/22, 1923, 1940). All the characteristic peculiarities such as the force of the great toe and its fixation in adducted position, the shortening of the other toes, the development of the heel, the restriction of the mobility of the tarsal joints, etc. may be understood only when regarded as static and dynamic effects of the body-weight bearing directly on the foot in consequence of the acquired erect posture. Such a transformation, however, can be completed only if the other parts of the limb and trunk itself are also adapted to the altered plan. All specific human particularities of the pelvis and leg, indeed, conform to the mechanic needs of the upright posture (Weidenreich, 1913), and the same holds good for the spine and, last but not least, for the skull (Weidenreich, 1924).

In comparing any bone of some significance in the construction of the human skeleton with the corresponding element of apes, it becomes evident that specific differences as may be observed are due to special adaptations and that only in those cases in which the bones serve the same purpose, a greater conformity exists. The heel bones of man and orang-utang differ essentially because of the entirely unlike construction of the foot, whereas, for instance, the lower extremity of the human humerus diverges only insignificantly from that of the chimpanzee, since the function is completely the same in both cases.

The dependence and correlations which become evident by such a comparative analysis of the body are, of course, also manifest in the phylogenetic evolution. It is an entirely inconceivable idea that each morphological unit should have developed independently from all others and from the body as a whole, as an isolated and incidental variation, subsequently tested as to its feasibility for the organism. The more peculiarities of an organism will be understood as "anatomical constructions" as Hans Böker (1936) called them, the more will it be realized that the way of dissociating the organism into an assemblage of individually independent structural units, adapted but secondarily by selection, must meet with failure. One wonders how it was possible once to count Wilhelm Roux' papers: "The struggle of the parts within the organism" (1881), an essential progress in our knowledge of nature. Roux extended Darwin's principle of evolution to all individual parts of the organism, imagining that even the cells should fight against each other constantly in competition for food stuff and the final survivor should then determine the definitive form of the organs of the body.

August Weismann's germinal selection (1904) represents the climax of such a supposition. According to that theory, the germ-plasm should be comprised of individual and different living units, the so-called "determinants", that is to say, primary constituents of each particular element of the organism, in the sense that these elements could not develop if their determinants were absent from the germ-plasm and that they would deviate if the determinants were differently composed. "If the germ-plasm be a system of determinants, then the same laws of struggle for existence in regard to food and multiplication must hold sway among its parts which hold sway between all systems of vital units—among the biophors which form the protoplasm of the cell body, among the cells of a tissue, among the tissue of an organ, among the organs themselves, as well as among the individuals of a species and between species which compete with one another." This means that the struggle of the determinants for the best food should finally weaken some and strengthen others, and as a consequence thereof the organs or parts of the body depending with their

existence upon the primary constituents (the determinants) would wane or flourish, respectively.

Weismann's ideas have been widely accepted in genetics, although their final consequence, namely the theory of the course taken by evolution being already decided within the germ-plasm by accidental selection of "determinants", may now hardly have many followers. Yet, the tendency to divide the body into its minutest particles and define both nature and origin of the organisms exclusively from this perspective has survived. The facts offered by comparative anatomy, or even its methods, in some quarters are regarded as unsuitable for an explanation of any evolutionary processes. Evolutionary series ascertained by palaeontological methods are discarded as insignificant. Exclusively genetical experiments carried out on living organisms of today should be able to disclose how man developed from the original type in the course of millions of years. There are scientists who appear to be unconscious of the fact that, in spite of all the endeavours of the last decades, one has until the present not surpassed beyond revealing general rules of heredity and its mechanism involving mainly characteristics of secondary importance. It is, however, evident that by this method the circumstances which caused a phylogenetic alteration of a given type in the past can never be reconstructed. For even if crossing between two types differing from each other fundamentally should happen some day, only the manner in which the already existing special features of either type may behave could be brought to light. But we would be unable to learn anything about their proper formation. This, I believe, demonstrates the limited boundaries of the methods applied in genetics.

On the other hand, an unrestricted field lies open to comparative anatomy, if it proceeds more than hitherto to comprehend the organisms as unitary constructions, and to unveil the leading principle thereof. Then it will be found that the individual characteristics cannot be understood as such but merely as symptoms of a certain plan of organization and not at all as independent formations.

This study will demonstrate that it is possible by mere morphological comparison to disclose parallels of evolution produced by natural variations and thus recognize the real determinants of evolutionary phenomena. It deals with the morphological problem of the phylogenetic transformation of the human skull and the general principles underlying this process.

I. Obliterations and Persistence of the Cranial Sutures

Studies dealing with the individual age of fossil man and the duration of his life are based on the assumption that the conditions serving as a criterion for estimating his age are the same as in modern man. One of the main means to judge the age is the behavior of the cranial sutures. As the approximate time of life at which they obliterate in modern man is fairly well known, it can be supposed that a fossil skull exhibiting the same suture conditions may have belonged to an individual of about the same age. Yet, one reservation is to be made. In great apes the sutures close much earlier than in modern man. In primitive fossil types, therefore, the suture closure may have occurred earlier in accordance with the phylogenetic stage of the type. If the cranium only is preserved, a correct determination of age merely on the basis of the suture conditions is impossible. For pronounced obliterations in such a case could also indicate that the individual in question was of rather advanced age. Some aid can be derived from the conditions of the teeth. Well worn

teeth generally indicate an advanced age, while those with only a slight degree of attrition indicate relative youth.

Neanderthal man, as far as cranium and teeth of one and the same individual are preserved, supplies no evidence that he differed essentially from modern man with regard to the age limit of suture closure. In all cases no distinct disproportion exists between the conditions of sutures and teeth. In *Sinanthropus* it is somewhat different. As I have already shown elsewhere (1939), there are two skull fragments comprising the temporal and adjoining bones—Skull H and Skull J—in which the squamo-parietal sutures are completely fused. In the first mentioned skull it is also true of the masto-occipital and lambdoid sutures. Teeth which could be attributed to these skulls with absolute certainty are not available. As the squamo-parietal and lambdoid sutures begin to obliterate very late in life (cf. Schwalbe, 1901; Frédéric, 1906; Todd and Lyon, 1924/25; Krogman, 1939), Skulls H and J with these sutures completely fused prove an advanced age. In assuming that the duration of life was much more limited on account of the more primitive conditions than is true today, we may be inclined to believe that complete closure of the cranial sutures is not a sign of advanced age, but rather indicates an earlier obliteration. In *Sinanthropus* Skulls I and II of Locus L (both belonging to adult individuals) a part of the dentition is preserved, thus permitting a comparison of the degree of wear with the conditions of the cranial sutures. In Skull I the coronal suture is fused and likewise the sagittal suture in its bregmatic section, while all the other ones are open. This individual (probably a male) may, therefore, have been about forty years old. In Skull II the coronal, sagittal and lambdoid sutures are fused, but those of the temporal bone open implying that this individual (probably a female) apparently was older, being about fifty years old. The teeth in both cases show extensive wear. In Skull I the degree of attrition of the upper premolars and second molars corresponds to No. 7 of the scale used in my attempt to classify the state of wear (1937) and the upper canine to No. 4. In Skull II the corresponding number of the upper teeth are: median incisor, premolars and first molar No. 7, canine and second molar No. 6 and third molar No. 5. These numbers correspond approximately to No. III and No. IV of Broca's classification of attrition.

Thus, the behavior of *Sinanthropus* fails to supply an adequate answer to the question whether his sutures close earlier than in modern man. The only evident difference consists in the sequence of the obliteration. In modern man the sagittal suture closes first and the coronal suture follows, whereas in *Sinanthropus* the sequence is reversed. This fact is worth noting, for according to Bolk (1913) in none of the primates he examined did he observe the coronal suture to close first, except in *Chrysothrix*.

The conditions are quite different in *Pithecanthropus* skulls. According to Dubois' (1924) and Weinert's (1928) statements Skull I exhibits the following particularities: The coronal suture is fused but partly recognizable, the same is true of the sagittal suture. The conditions of the lambdoid suture are not quite clear but it is evidently fused. Only the squamosal suture seems to be partly open. At any rate, the main sutures of the cranium are ossified but not completely obliterated. The age of the individual can, therefore, be estimated to be about fifty years. In von Koenigswald's (1938) *Pithecanthropus* Skull II the coronal, sagittal and lambdoid sutures are completely obliterated, but their course can still be determined with the aid of X-ray photographs. The squamosal suture is fused but partly visible and the same is true of the masto-occipital and the spheno-temporal

sutures. The spheno-parietal suture is obliterated. Judging by the conditions in modern man, this individual must have been at least seventy years old. Yet, a skull showing such a complete suture obliteration is very rarely found in mankind of today, especially when we take into account that Skull II probably belonged to a female individual, for in females the sutures admittedly close later than they do in males. Unfortunately, in these two cases there are no teeth available which could serve as a more reliable basis for correct determination of the age.

The latest discovery of *Pithecanthropus* Skull IV which consists not only of the fragments of the greatest part of the cranium including the base, but also of the upper jaw with ten teeth still *in situ*, fills the gap existing hitherto in this respect. Preliminary notes referring to the find of this skull and the upper jaw have already been published by von Koenigswald and myself (1939) in a joint article and by von Koenigswald (1939) as well as by myself (1940) in special papers. Due to the fortunate circumstance that von Koenigswald just happened to be visiting and working on the other *Pithecanthropus* material at our Cenozoic Research Laboratory in Peking when the skull was discovered, I was able to participate in its preparation and definition and to examine the special conditions of the skull with regard to sutures and teeth. The lambdoid suture is completely obliterated, the same is true for the sagittal suture, only in the bregmatic section can the latter still be distinguished to some extent on the outer side of the cranium. Despite the fact that the region on either side of the squamosal suture is badly crushed and partly dislocated, it is still possible to recognize a complete obliteration of the sutures. The masto-occipital and the squamo-sphenoidal sutures are completely fused, but some slight vestiges of the masto-parietal suture are preserved. Therefore, on the basis of the evidence supplied by the conditions of the sutures and their appearance in modern man, the age of this *Pithecanthropus* individual may be estimated to be about eighty years. However, it must be borne in mind that, even in recent mankind, skulls of such an advanced age show but rarely such a high degree of obliteration of all the sutures. The upper jaw, as far as its sutures are concerned, completes the picture, the sagittal and transversal palatine sutures being also entirely fused. In full contrast to the behavior of the sutures, the teeth are surprisingly little worn, especially the last erupted ones. According to the scale I used in classifying the degree of wear (1937), their attrition corresponds to Nos. 2 and 3 which fact proves that the individual must have been relatively young. If this be so, the only plausible conclusion drawn from the difference between the behavior of the sutures and the teeth is that this individual must have been much younger than the sutures indicate. In other words, the sutures in *Pithecanthropus* close much earlier than in modern man. *Pithecanthropus* thus resembles the anthropoids in this respect.

There is, of course, another alternative worth noting. May it be supposed that the teeth of *Pithecanthropus* are less worn than the teeth of *Sinanthropus* or those of modern man of the same individual age? The material of *Pithecanthropus* teeth available thus far is rather poor, especially of such teeth as could have served as a reliable basis for the estimation of age. Although the occlusal surface is somewhat eroded in the teeth (second premolar and all three molars) preserved in the adult *Pithecanthropus* mandible B (von Koenigswald, 1937), it is nevertheless possible to determine the degree of abrasion. All the teeth are relatively slightly worn, corresponding approximately to Nos. 3 to 5 of our

scale; but since cranial bones belonging to this jaw are lacking, there is no way of comparing the condition of the teeth with that of the sutures.

According to the character of the sutures of *Pithecanthropus* Skull IV, this individual shows a much more advanced age than *Sinanthropus* represented by Skull II of Locus L. The upper teeth of the former skull, however, show considerably less wear than the corresponding ones of the latter. This deviation could have been caused by a different type of diet. The information we have about the nutrition of *Sinanthropus* strongly suggests that he subsisted chiefly on meat. No indication of any kind is available as to the food habits of *Pithecanthropus*. But, provided that he really was feeding on fruit, in contrast to *Sinanthropus*, the conditions of his teeth can still not be explained by a mere difference in diet. For the present day anthropoids are also frugivorous but their teeth, as a rule, show considerable wear when they reach an advanced age.

It is a well known fact that in modern man the abrasion increases with age. This is particularly true of primitive races. Campbell (1939) who studied these conditions on living Australian aborigines gives the following figures:

TABLE I

ATTRITION OF TEETH IN AUSTRALIAN ABORIGINES

Age of 300 Living Australian Aborigines	Degree of Attrition in Percentage			
	I	II	III	IV
12–20 years	55.5	44.5	—	—
20–29 years	44.0	44.0	12.0	—
30–49 years	11.3	32.1	43.4	13.2
50 and over	1.2	18.3	46.4	34.2

It can be gathered from this list that the wear of the teeth is a general occurrence in aged individuals, and although minor degrees of attrition may be found to a certain extent among them, the overwhelming majority shows strongly worn teeth. Campbell used Broca's scale of attrition. Degree "I" means "enamel worn without cusp obliteration or dentine exposure". This corresponds approximately to the conditions of the teeth of the upper jaw of *Pithecanthropus* Skull IV.

From the behavior of sutures and teeth in this single case it is not possible, it is true, to deduce with absolute certainty that in *Pithecanthropus* the sutures close much earlier than in modern man. But considering the fact that all adult *Pithecanthropus* skulls at our disposal up to the present, namely Dubois' Skull I and von Koenigswald's Skulls II and IV—the two former representing female individuals and the latter a male—exhibit a preponderance of suture closure which is incontestably uncommon among modern man, we feel justified in claiming that *Pithecanthropus* differs from recent man in this respect and behaves like an anthropoid.

Pithecanthropus thus reveals a new anthropoid character, hitherto disregarded, which is in full accordance with others of the same nature, thereby testifying to the primitiveness of this Prehominid. Viewed from the phylogenetic standpoint we could expect an early fusion of the sutures in such a stage of evolution because of its specificness for the great

apes. But another question arises. Bolk (1913) was first to draw attention to the fact that a premature closure of the cranial sutures, so characteristic of the anthropoids, does not occur in lower monkeys. In these cases and, in particular, in the Platyrrhinae the sutures have the tendency to remain open. Man, therefore, showing the same trend, joins the lower monkeys but not the great apes. Bolk attempted to express in figures the degree of suture closure, lower figures implying a lesser degree and higher figures a correspondingly higher one. The left side of Table II shows, in general, the figures and their sequence.

TABLE II

SEQUENCE OF DEGREE OF OBLITERATION OF CRANIAL SUTURES AFTER BOLK (1913)—LEFT SIDE—AND THE RELATION OF BRAIN-WEIGHT TO BODY-WEIGHT AFTER M. WEBER (1887)—RIGHT SIDE

Genus	Degree of Obliteration after Bolk	Relation of Brain-Weight to Body-Weight after Weber
Chrysothrix	1	1 : 17
Hapale	2	1 : 26.5
Cebus	15	1 : 18.5
Mycetes	39	(1 : 51.5)
Macacus	46	1 : 69
Siamang	62	1 : 73
Semnopithecus	66	1 : 116
Orang	88	1 : 194
Gorilla	93	(1 : 212)

It is rather difficult to offer any satisfactory explanation if this problem is approached only from the phylogenetic side. Modern man follows the rule existing in lower monkeys and not such in anthropoids as may have been expected, whilst his most primitive ancestor conforms to the latter. But it appears as if man had changed his character when, in the course of evolution, he passed through a type similar to that of the present day anthropoids. Of course, we do not know how the conditions of the cranial sutures were when man was still in a stage preceding that of the great apes. Bolk advanced two somewhat differing interpretations: first (1913), that the strong muscular force and the heaviness of the facial skeleton of the skull of anthropoids require a continuous system of cancelli within the wall of the brain case causing an early obliteration of the sutures, whereas in man the sutures should be able to persist on account of the much weaker muscles and the less heavy facial skeleton. Later (1915), he considered the growth of the brain responsible for the persistence of the sutures in man. The sutures were unable to unite before the brain had attained its final size. Therefore, in apes, they should close immediately after the cessation of their physiological function, namely that of keeping the brain case open, whereas in man the growth of the brain should last longer and more than this: the suture should even persist for a long time after the brain has ceased to grow. Neither of these interpretations can be wholly accepted, though both of them do contain a certain amount of truth. Notwithstanding this fact, the primary question concerning the discrepancy in the supposed evolutionary line of man, namely modern man returning to the behavior of more primitive stages after having passed through the advanced one of anthropoids, remains unsolved. As the

matter stands, circumstances leading to the closure of the cranial sutures or to their persistence apparently do not necessarily depend upon the course of evolution. There must be some special factors which determine those conditions.

Before we enter into a discussion, it is essential to consider another phenomenon which may have a bearing on the conditions of the sutures, namely the thickness of the bones forming the cranium. It is a well known fact that in all the skulls of fossil man these bones are markedly thick, generally many times thicker than the corresponding bones of modern man. In Table III the thickness of the four main bones of the brain cases of *Pithecanthropus*

TABLE III

THICKNESS OF THE INDIVIDUAL BONES OF THE CRANIUM OF PREHOMINIDS AND MODERN MAN IN MM

	Pithecanthropus		*Sinanthropus*				Modern Man
	II	IV	E	D	H	L III	
FRONTAL:							
Tuber	10.5	—	5.0	10.0	—	5.5	5.8–6.3
Glabella	23(?)	—	19.5	22	—	28.5	11.3*
PARIETAL:							
Tuber	9	6(?)	11	11	—	9	2–5
Ant. sup. angle	8.5	5.5(?)	10	9.5	—	8	5.5
Post. sup. angle	13	9	14	10	—	8.5	6
Post. inf. angle	17	12	15	13	13	13.8	4.5–5.2
OCCIPITAL:							
Sup. portion of the squama	12	14	14	8.5	—	9	6–8
Opisthion	17	21	17	—	—	13.5	5.7*
Middle portion of the nuchal region	17	15	15.5	—	—	12	3–4
Middle of the cerebellar fossa	4	5	—	—	4	4.5	1–1.8
TEMPORAL:							
Middle of the squama	7.5	7.5	10.5	—	10	7	1.3–2.5

* The figures referring to modern man are after R. Martin (1928); those with an asterisk after Todd (1924).

and *Sinanthropus* are listed, together with the average measurements of modern man. As the average capacity of the *Pithecanthropus* skull amounts to about 900 cc and that of *Sinanthropus* to about 1000 cc, there is no doubt that the decrease in the thickness of the wall of the brain case has something to do with the expansion of the cavity. Although such a thickness is specific to man, the thickness of the middle of the parietal bone of anthropoids, for instance, hardly exceeds 5 mm, there is a significant difference between those types of monkey or apes with a high degree of obliteration of the sutures and those with a minor one (cf. above). In the latter, the bones are much thinner than in the former. For example, a male *Saimiris*, in which the degree amounts to 1 or 2 (cf. Table II), the parietal

bone is only 0.6 mm thick, while in a male *Alouatta* with a degree of about 39 the thickness is twice as much. We have to come back to this question later.

Literature dealing with closure and persistence of the sutures is rather extensive. But the question as to why the fusion of the suture in man takes place so late in life has as yet not been adequately and wholly satisfactorily answered, especially when compared with what is known of anthropoids. Of all the eventualities discussed by Bolk (1931, 1915, and 1919/21 *a* and *b*), his suggestion that the brain plays an essential rôle deserves special attention. But all the special investigations undertaken on human material to discover certain relations between roominess of the cranial cavity or form of the cranium and date of closure resulted in failure (Todd and Lyon, 1925). There apparently is no distinct difference in this respect between skulls with a large capacity and those with a small one. The only fact which can be considered as proved is that the sutures in general are closed later in females than in males, although their cranial capacities or brain volumes do not exceed in absolute measurements those of the latter (cf. Frédéric, 1906).

The most suggestive argument is found in the attempt of bringing the persistence of the sutures in man into correlation with the size of the brain. As mentioned above, Bolk voiced the opinion that the growth of the brain should last longer in man than in anthropoids and the sutures close correspondingly later. Thus, we must determine whether there is any evidence that the human brain really increases in size as long as the sutures are patent, and, secondly, whether the growth of the anthropoid brain ceases earlier than in man, coinciding with the earlier closure of the sutures. The answer is of considerable interest even beyond the immediate question. We know fairly accurately at what age the sutures of the human vault begin to unite. According to Frédéric (1906), Todd and Lyon (1924/25) and Krogman (1939) the sagittal and the fronto-sphenoidal sutures are the first to fuse at the age of twenty-two, followed by the coronal and lambdoid sutures at twenty-four and twenty-six, respectively, the spheno-parietal suture being the last at twenty-nine. The circum-meatal sutures start at the age of about thirty years. These figures, however, indicate only the earliest time limits as the start may be delayed by many years. Indeed, there are cases reported in the literature in which the sutures were found patent, despite an age of seventy or more years. On the other hand, we do not have the slightest knowledge whether the beginning of the union of a suture may have any arresting effect on the growth of the brain. It is even imaginable that the brain and the cranial cavity expand, in spite of the sutures being completely closed. Although it is almost generally assumed that the cranium can be widened only by apposition of new bony substance along the cranial sutures, there are still some indications that the cranial cavity also may become enlarged by erosion on the inner table of the cranium and by corresponding apposition on the outer one (cf. Weidenreich, 1930). In any case, the question cannot be decided merely on the basis of the conditions of the sutures.

Frédéric (1906) considers it ascertained that the growth of the human brain reaches its highest point at the age of twenty years but should continue to grow "imperceptibly" up to the age of thirty-five. If, however, all available data seemingly in support of this statement are examined closely, we arrive at quite a different conclusion. In case there is actually an enlargement of the brain after a certain age has been reached, the only reliable way to assert it is to determine the brain-weight in all the ages concerned. We are indebted to Marchand (1902) and Handmann (1906) for series of measurements which

prove that the brain of males in general ceases to increase in weight at the age of twenty years, whilst that of the females stops already at the age of sixteen to eighteen years. Even if in some cases the growth should continue, such a prolonged development can be considered insignificant. On account of these facts, the beginning of the closure of the cranial suture really seems to mark the final phase of brain growth. Nevertheless, it still remains dubious whether an immediate relation exists between the two phenomena. As already mentioned above, the sutures close later in females or, at least, at the same time as in males. This is somewhat contrasting to the results yielded by the brain-weight. On the other hand, if the time of the union and obliteration of the sutures as a matter of fact are conditioned by the cessation of the brain growth, it is difficult to understand why in almost all cases it requires so many more years until all the cranial sutures have really fused and why, in contrast to the great apes, their complete obliteration is relatively rare. In certain cases, not infrequent, the sutures are still patent at an age at which, according to Marchand's statistics, a considerable decrease of brain-weight must already have taken place.

In this connection, another phenomenon is worth noting, namely the occasional persistence of the metopic suture in human skulls. The persistence of this suture is not at all exceptional as surmised by numerous authors. If there is a general tendency to keep the cranial sutures open, there is no reason why this should not hold good for the metopic suture, too. In this case, we may expect that in great apes its occurrence is much more rare than in man. That this is really true can be gathered from Remane's (1925) figures. According to this author, the persistence of the metopic suture has never been found in chimpanzee (see below), while in orang-utang its occurrence amounts to 1.0 per cent and in the gorilla to 2.4 per cent. In man, however, the suture is much more frequent as may be seen from Bolk's (1921/21b) and Ashley-Montagu's (1937) lists (Table IV), the average of the entire mankind being about 6 per cent and, strangely enough, as especially stressed by Bolk, more frequent among higher civilized races than among primitive ones.

It is only natural that the persistence of the metopic suture was also brought into correlation with the growth of the brain. R. Martin (1928) supposes that the growth of the frontal part of the human cranium more intense and thus exerting a stronger pressure upon the interior than in the case of the great apes should prevent the regular union of the metopic suture. Bolk, however, differs from Martin. Using as basis the erroneous assumption that a metopic suture should never occur in great apes, he believes the tension of strong temporal muscles, actually existing in anthropoids, causes the two original halves of the frontal bone to fuse early, while a diminished tension as manifested in modern man eliminates such a tendency.

It is interesting to note that of these two explanations one resorts to an internal and the other to an external force. Both, however, are incorrect. For there is no evidence that a strictly localized expansion, like the supposed enlargement of the frontal lobe, should affect only one suture. On the other hand, I was able to demonstrate (1936) that a preferential enlargement of the frontal lobe in the course of human evolution, considered a certainty by the majority, in reality is a legend. The brain expands mainly in its entirety and in all directions. In addition, the most favored region is not the frontal lobe but the parietal lobe, whilst the most privileged direction of expansion is not in breadth as Martin's explanation implies but in height. In regard to the temporal muscle, neither its strong nor

weak development can have any influence on the behavior of the metopic suture as was shown by Remane (1925), for the suture is not absent at all in anthropoids as supposed hitherto but occurs in 2.4 per cent in the gorilla and in 1 per cent in the orang-utang. Only in the common type of chimpanzee has a persistence of the suture never been observed (Ashley-Montagu, 1937, cf. below). I may add that in *Sinanthropus* Skull II of Locus L the metopic suture is well preserved, notwithstanding that the other sutures of the vault have already closed, while the presence of heavy supra-orbitals testifies to the continued effectiveness of the temporal muscles (cf. Weidenreich, 1937a). Bolk's theory, therefore, contrasts with all the facts.

TABLE IV

PERCENTAGE OF OCCURRENCE OF METOPISM AMONG VARIOUS RACES OF MODERN MANKIND, *A* AFTER BOLK (1919/21b), *B* AFTER ASHLEY-MONTAGU (1937)

A	
Australian aborigine	1.0
Negro	1.2
Malayan	2.6
Papuan	4.3
Bavarian	6.4
Slav	6.4
Alsatian	6.5
Swiss	7.1
Hamburgian	9.5
Scotch	9.5
Dutch	9.5
Parisian	9.9
B	
Polynesian	0.9
Melanesian	2.0
Mongolian	6.5
European	8.3

A close examination of all available data offered no indication that the retarded closure of the cranial sutures of modern man can be considered as directly dependent upon a prolonged growth of the brain. As mentioned above, certain authors believe that the brain of anthropoids ceases to grow much earlier than that of man, and the sutures should behave correspondingly. We owe an excellent study on this question, as far as the growth of the brain is concerned, to Zuckerman (1928). From his references to the literature, it can be gathered that the opinions differ widely. While some authors found that the growth already stops by the end of the first year of life, others hold the view that it continues to grow considerably longer, at least up to the complete eruption of the second set of teeth. According to Zuckerman's own investigations on the chimpanzee, the average cranial capacity is the same for adults as for that group in which only the third molar of the permanent dentition is unerupted. This means that in chimpanzee the brain growth practically ceases near the final phase of the permanent dentition. But at any rate, the increase of the brain in these later stages is rather insignificant. Zuckerman distinguishes three such stages, namely: the intermediary stage between the eruption of the first and

third permanent molars; the stage with the third molar unerupted and, finally, the adult stage. Table V shows the results obtained by that author.

TABLE V

CRANIAL CAPACITY OF JUVENILE AND ADULT CHIMPANZEE (AFTER ZUCKERMAN, 1928)

	Cranial Capacity	
	♂	♀
Intermediary stage	402.0 cc	357.2 cc
M3 unerupted	399.0 cc	384.5 cc
Adults	399.5 cc	384.5 cc

It is interesting that in these cases measured by Zuckerman only the females show an increase of the capacity, whereas the males even exhibit a decrease. These figures prove that the brain growth ceases after the eruption of the second molar. As to the age of the chimpanzee, Zuckerman states that he arrived at the conclusion that all the available data indicate that the time limit of tooth eruption of the chimpanzee is the same as in man, that is to say, the first permanent molar erupts between five and six, and the last molar does not erupt before fifteen and probably later.

It is to be regretted that up to date no reliable data are available regarding the brain growth of the gorilla and the orang-utang. Selenka (1898) claims that the capacity of orang skulls increases 14 to 20 per cent after the complete eruption of the deciduous dentition and 3 to 6 per cent after the eruption of the second permanent molar. Duckworth (1915) merely states that in the gorilla but a slight degree of brain growth could be observed after infancy.

It may be deduced from all these facts that there exists but a small difference between man and anthropoids with regard to the duration of the brain growth. While in the latter the brain growth usually stops at the age of 10 to 15 years, in man the growth continues up to 18 to 21 years. According to Marchand's (1902) and Handmann's (1906) figures, the weight of the human brain at the final phase of the deciduous dentition amounts to 87.5 per cent of the full weight in males and to 96.7 per cent in females. If Zuckerman's figures are reliable, the same percentage should hold good for the chimpanzee but with a higher percentage for males.

As to the relation between the suture closure and brain growth in anthropoids, St. Oppenheim (1911) stands alone in inferring a continuation in brain growth from the persistence of the sutures following the complete development of the deciduous dentition. Zuckerman's attitude hereto is somewhat strange. Although denying the existence of any evidence inferring a cessation in cranial growth at the time of sutural coalescence, yet he seems to reserve the possibility of a continuation of such a growth, regardless of the obliteration of the sutures. For the remainder, I refer to previous discussions of this question.

To summarize the results obtained by this enquiry, it may be stated that there is not the slightest indication to suggest a correlation between suture closure and brain growth. It is most regrettable that information on brain growth is lacking of those platyrrhine monkeys which according to Bolk's list (cf. Table II) display but a slight tendency towards suture obliteration. But it may certainly be reasonably assumed that the enlargement

of the brain does not continue beyond the date of completion of the permanent dentition. Even if we should admit that in certain known anthropoids the closure of the sutures coincides approximately with the cessation of brain growth, there still remains a distinct discrepancy between the two occurrences in man. We must, therefore, seek for a more acceptable explanation.

II. Dwarfs and Large Types

In his study on prehistoric dogs Studer (1901) called attention to the fact that a great difference could be observed in the appearance of the skulls of dwarf dogs, on one hand, and of large dogs, on the other. The former, as postulated by Studer, should retain juvenile characters, in the smallest types even embryonic features. The skull of a very old dwarf pinscher illustrated by that author shows a thin-walled globular cranium without crests but with frontal and lateral fontanels preserved. In accordance therewith the face is small and frail. Schmitt (1903), Klatt (1913, 1921) and later Wagner (1929) described the same particularities as specific to dwarf dogs. Large dogs contrast by showing a narrow elongated cranium with pronounced crests and a similarly elongated face. This appearance of the skull is considered typical for the dog and, so to say, normal, while that of the dwarf dogs is considered a more or less abnormal form—as a sign of achondroplasia or something similar to it. Stockard (1931) referring to bulldogs and Pekingese remarks briefly: "These types are often hereditary but, in all cases, are associated with peculiar reactions of the glands of internal secretion."

Let us put aside for the moment the question whether dwarfism is caused by some disturbance in the system of internal secretion or whether it can be defined satisfactorily as a mere retention of embryonic characters. More interesting is the purely morphological aspect of the problem. There is no doubt that a skull of a Pekingese or a King Charles spaniel, on one hand, and that of an Irish wolfhound or a St. Bernard, on the other, display very essential differences which are not confined to the size but involve the structure of the skull as a whole as well as its details. Not less important, however, is the fact that these small and large types represent only the extreme stages of a continuous series of types with such intermediate ones between them, not only in respect to the size but also in regard to structure. In Figs. 1–5 three skulls of adult dogs are represented which illustrate three different types of dogs, namely one of the smallest dwarf types, a King Charles spaniel (*A*); one of the largest types, an Irish wolfhound (*C*); and an intermediate type, an English bulldog (*B*). The last, not being absolutely intermediate but somewhat closer to the dwarf, nevertheless shows all the characteristics of such a middle form. To facilitate the comparison, skulls *B* and *C* have been reduced to one basic line corresponding to the biauricular breadth of skull *A*. In all cases, the skulls are orientated in the suborbital-porion plane.

Figure 1 shows the three skulls in lateral view. The cranium which extends about from the nasion (*n*) to the rear end is represented in skull *C* by a long and relatively low body. The lateral wall of the orbits is absent as is the case in all carnivorous skulls, but its position at the wall of the cranium is marked by a very pronounced triangular postorbital process (*pp*) which projects considerably over the surface. This process continues backwards with a heavy crest (*sc*) increasing in height toward the occipital region where it communicates with a corresponding nuchal crest (*nc*). The lateral surface of the cranium

proper is formed by two rounded elevations, an anterior and a posterior one. These elevations are separated from each other by a distinct depression which coincides with the course of a rough line, the completely obliterated coronal suture. As the vertical view of the skull reveals (Fig. 2, *C*), the anterior elevation is rhomboid-shaped, its angles repre-

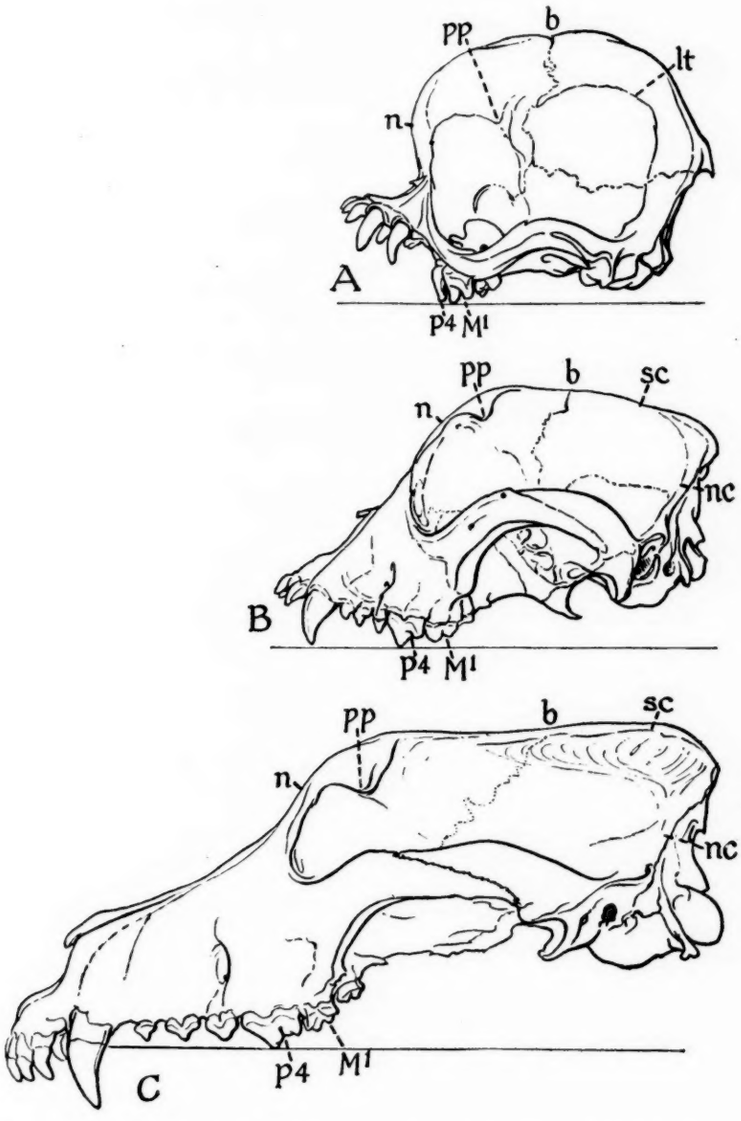

FIG. 1. Skulls of dogs of three different races of various size. Lateral view. Abbreviations: *b*, bregma; *n*, nasion; *nc*, nuchal crest; *pp*, postorbital process; *sc*, sagittal crest; *lt*, temporal line. *A*. Adult female King Charles spaniel. Coll. A.M.N.H. (American Museum of Natural History) no. 19182. 3/4. *B*. Adult English bulldog, probably male. Coll. A.M.N.H. no. 69453. About 1/3. *C*. Adult male Irish wolfhound. Coll. A.M.N.H. no. 90250. 1/4. (The skulls *B* and *C* have been reduced to the biauricular breadth of the smallest of the three—skull *A*.)

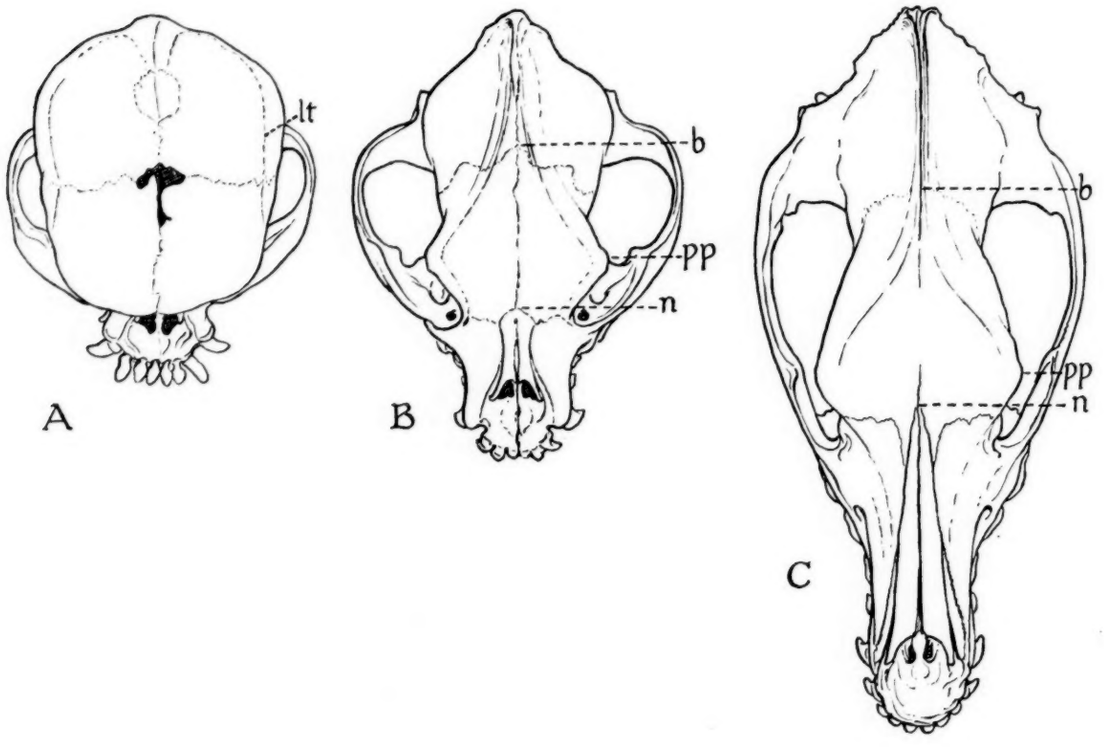

FIG. 2. The same three skulls as in Fig. 1 in vertical view. Reduced to the same size as above.

sented by the postorbital processes on either side. The posterior one is much smaller and of ovoid form.

The skull of the dwarf dog (*A*) offers quite a different aspect. The cranium is short and high and bulging. The frontal part, tuber-like, projects outwards and the same is true of the occipital part. The postorbital process (*pp*) is reduced to a faint triangular pattern on the lateral surface. There are no traces of crests, instead of which there is a fine temporal line (*lt*) running about halfway between the squamosal and sagittal sutures. Seen from above (Fig. 2, *A*), the cranium represents a unitary globule-like body with well marked frontal and parietal eminences. The coronal and sagittal sutures are patent and so is the metopic suture. The bregmatic region is occupied by a wide fontanel of irregular form.

The fundamental differences between skulls *C* and *A* are most marked when viewed from behind (Fig. 3). Skull *A* very strikingly exhibits its globular form. The greatest breadth is situated far above the biauricular plane. There are no crests or other superstructures, the temporal line (*lt*) being represented by a faint line. All the sutures are patent. On either side there is a small round asterion fontanel. The foramen magnum is surprisingly wide and developed particularly in a vertical direction. In skull *C* the cranium proper appears in a narrowed triangular form, its greatest breadth coinciding with the biauricular plane. The cranium is crowned by a high and thick crest. This crest ends at the front on either side in a large super-structure corresponding to the anterior

elevation and the postorbital process described above in lateral and vertical views. The sutures are obliterated and the foramen magnum is relatively small and especially developed in a transversal direction.

The skull of the English bulldog (Figs. 1–3, *B*) stands intermediate in regard to all these peculiarities. The cranium is considerably shorter and relatively broader than in the wolfhound, but there are still the two elevations and the super-structures, although much less pronounced. The cranium proper is somewhat wider and the sutures are still patent.

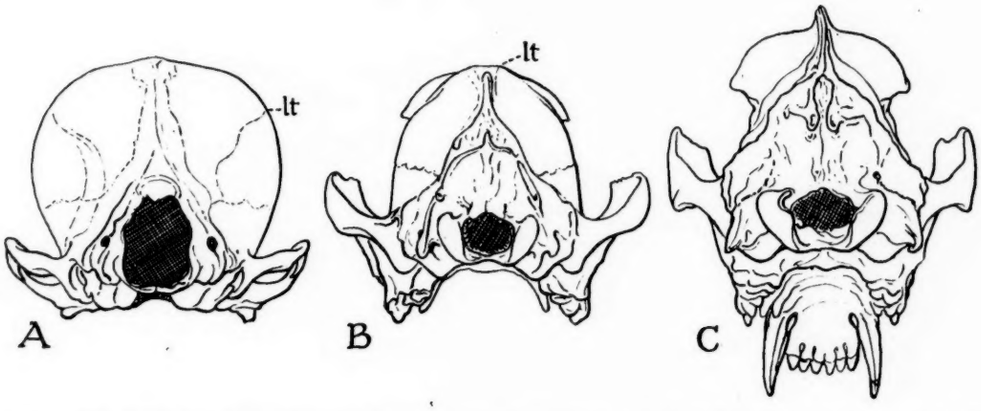

FIG. 3. The same three skulls as in Fig. 1 in occipital view. Reduced to the same size as above.

Studer (1901) and those accepting his conception were satisfied with the statement that dwarf dogs retain juvenile or even embryonic characters. But such a statement fails to cover the issue. The shape and size of the cranium is determined mainly by the roominess of the cranial cavity or, in other words, by size and expansion of the brain. It is a well known fact that small animals have relatively larger brains than large ones. This question will be fully discussed later. But as small animals have small skulls in accordance with the smallness of their bodies, the relatively large brain must occupy a much larger space in the reduced skull than it does in the case of large animals. In these the skull is large in correspondence to the size of the body, while the brain remains small. In the first instance, we thus have a marked disproportion between cranial cavity or cranium proper and the skull as a whole in favor of the brain; in the latter instance, the disproportion is reversed. The mutual relation between cranial cavity and skull can be illustrated best by tracing the space occupied by the cranial cavity within the skull as illustrated in Figs. 4 and 5. The olfactory recess, completely missing in dwarf dogs but very pronounced in large ones, appears as a median prolongation of the cranial cavity which extends in the direction of the nasion, not traced in Figs. 4 and 5. In the large dog (*C*), the cranial cavity takes up only a small part of the posterior upper region of the skull, while in the dwarf (*A*) it fills the entire cranium. This holds good in particular for the anterior region. In skull *A*, the cranial cavity extends far beyond the coronal suture, not only up to the nasion (*n*) but correspondingly also descends toward the maxilla with the result that the lateral wall of the cavity forms the entire medial wall of the orbit. The extension in length of the cranial cavity goes hand-in-hand with that in breadth, so that the form of the cranial

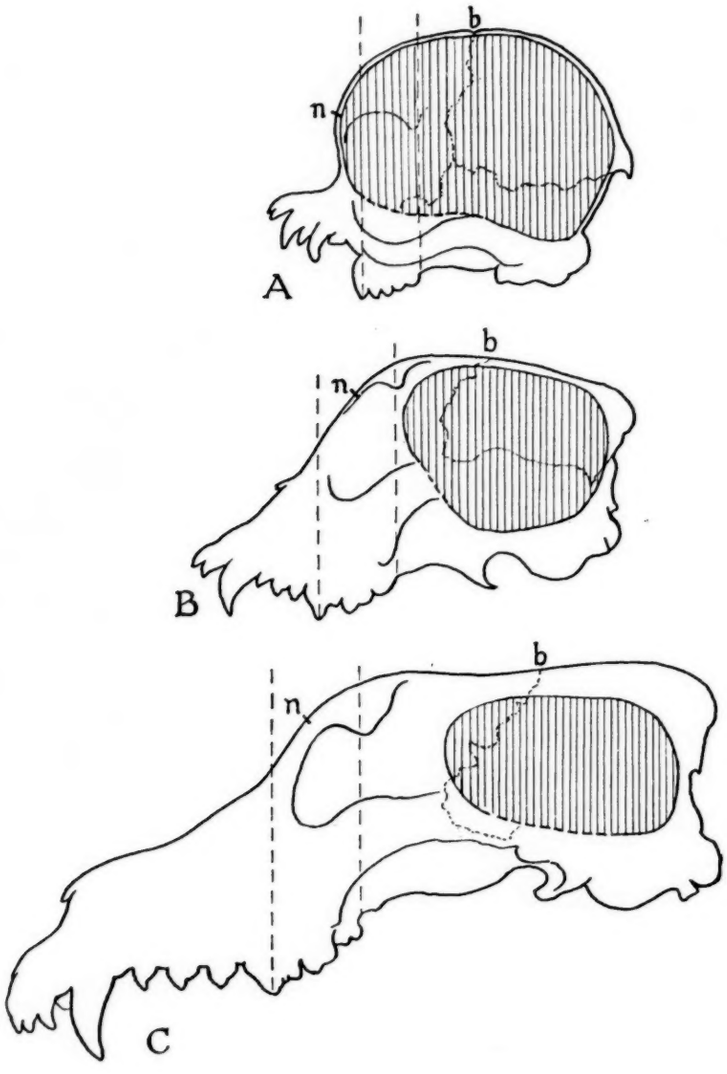

FIG. 4. The same three skulls. Outlines demonstrating comparative dimensions of the cranial cavities (shaded). Abbreviations: *b*, bregma; *n*, nasion.

cavity may be defined as "brachycephalic." In skull *C* the cranial cavity overpasses the coronal suture to a small extent only, the volume of the cranium in front of the anterior pole of the cavity being partly occupied by a large frontal sinus, partly by the nasal cavity. The sinus corresponds to the anterior rhomboid elevation described above. The orbit, as a whole, is situated entirely in front of the cranial cavity. There is no expansion of the cavity in breadth; it represents a "hyperdolichocephalic" form. As to the English bulldog (skull *B*), the conditions of the cranial cavity and its relation to the cranium correspond entirely to those of an intermediate form. But as the general character of the bulldog skull, as mentioned above, comes closer to that of the large dogs than to the dwarf dogs, the cranial cavity follows the same rule.

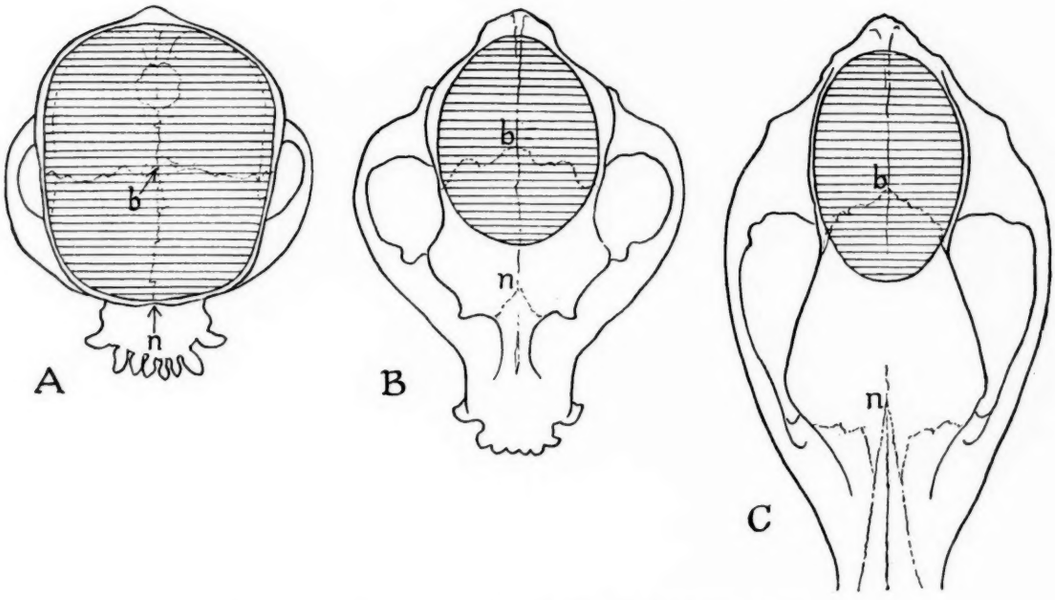

FIG. 5. The same as in Fig. 4 but viewed from above.

One particularity, however, deserves special attention. In large dogs the bones comprising the brain case are very thick. In the case of the Irish wolfhound, the thickness of the tuber region of the parietal bone amounts to about 3 mm. In the King Charles spaniel it amounts only to about 1 mm. This difference, together with the fact that the cranial sutures remain patent in dwarfs, regardless of their individual age, while closing early in large dogs, suggests the reasons underlying this diverse behavior. In the former cases, the skull as a whole is small and the bony material, designed to construct the brain case, is correspondingly scanty. The brain, on the other hand, is unproportionately large and requires, therefore, a more spacious covering than the bones can afford. In other words, I believe that the permanence of the sutures and the persistence of the fontanels in extreme cases constitute an indication of the cranial bones being incapable of meeting the greater requirement. The fact that the bones, in addition, are extremely thinned certainly points in the same direction.

As Figs. 1–3 show, the differences between dwarf dogs and large ones are not at all confined to the cranium but also involve the entire face. In extreme cases of dwarfism, the maxillae are enormously reduced in length as well as in height; this reduction, together with the strongly bulging forehead, produces a deep incurvation of the nasal bridge (Fig. 1, *A*), so that the upper jaw appears only as an unessential appendix of the cranium. In large dogs, on the other hand, the face is formed by a high and projecting maxilla. A special intermediary portion which is completely missing in dwarf types and consists chiefly of the frontal sinus joins the maxilla and the brain case (Fig. 1, *C*). It corresponds to the anterior elevation of the cranium already described above. The extraordinary shortening of the muzzle is particularly impressive when the skull is viewed from the basal side (Fig. 6). Then it becomes evident that the reduction is confined mainly to a decrease

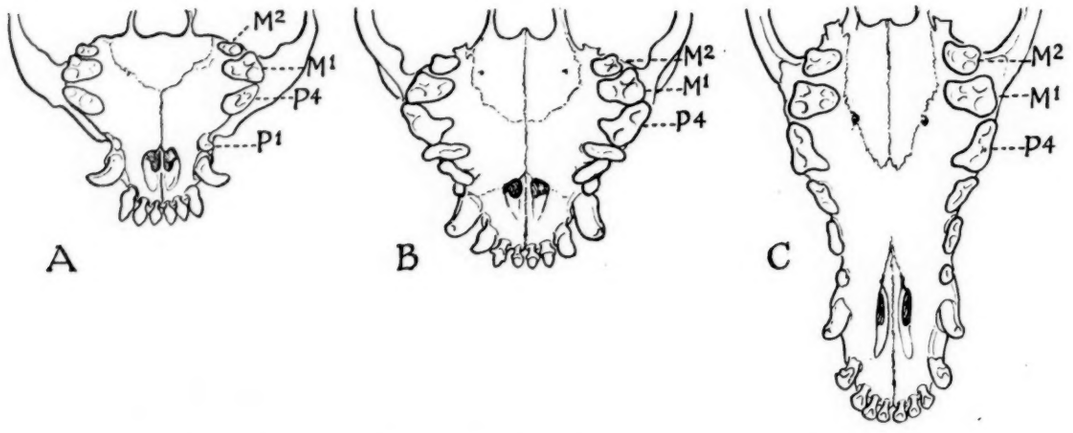

FIG. 6. Palate of the three skulls. The same reduction as in Fig. 1.

in length, while the breadth of the maxilla remains almost unaltered. The English bulldog (Figs. 1, *B* and 6, *B*) in this respect resembles more the dwarf types than the large ones.

There is a distinct correlation between the size of the cranial cavity and the total length of the skull. The greater the length of the cavity, the shorter the total length of the skull and conversely. This relation can be expressed in exact figures, when the length of the cranial cavity (opisthion to the anterior pole of the hemisphere) is compared with the total basal length of the skull (basion-prosthion).

TABLE VI

RELATION OF THE ENDOCRANIAL LENGTH TO THE BASAL LENGTH OF THE SKULL AND LENGTH OF THE FACE

	1 Endocranial Length	2 Basal Length (*ba-pr*)	3 Length of the Face (*n-pr*)	Index I $\frac{1 \times 100}{2}$	Index II $\frac{3 \times 100}{1}$
Irish wolfhound ♂ A.M.N.H. no. 90250	115 mm	252 mm	151 mm	45.6	131.0
English bulldog A.M.N.H. no. 69453	76 mm	119 mm	63 mm	63.8	83.0
King Charles spaniel ♀ A.M.N.H. no. 19182	52 mm	57 mm	5 mm	91.2	9.6

As Table VI shows, the length of the cranial cavity of the wolfhound amounts to 45.6 per cent of the total length of the skull but to 91.2 per cent in the spaniel. In correspondence therewith the length of the face of the wolfhound amounts to 131 per cent of the cranial cavity and of the spaniel to 9.6 per cent.

Wagner (1929) took numerous measurements on the various races of modern dogs, in order to get reliable figures suitable for a comparison with prehistoric races. From this material I selected those measurements involving the length of the skull, the length of the cranial cavity, the length of the face, the zygomatic breadth, the length of the molar row,

and the length of the femur. Table VII contains the absolute figures; Table VIII the indices computed thereof, and Table IX the corresponding figures and indices of the three special dog skulls of the collection of the American Museum of Natural History, used herein as examples. Wagner's figures are of particular value because they exhibit in each case the average of a greater number of male and female specimens, proving that a characteristic relation exists between the size of the entire skull and the size of the cranium proper

TABLE VII

MEASUREMENTS OF THE FEMUR LENGTH AND SKULLS OF VARIOUS RACES OF DOG
(AFTER K. WAGNER, 1929)

	1 Total Length of the Skull (*op-pr*)	2 Basal Length (*b-pr*)	3 Endo-cranial Length	4 Length of the Face (*n-pr*)	5 Length of the Row of the Lower Molars	6 Zygomatic Breadth	7 Length of the Femur
Wolf	254.6	221.2	106.6	148.1	96.3	139.6	—
Irish wolfhound	270.0	239.0	116.0	161.0	—	130.0	277.0
St. Bernard	250.0	223.0	105.7	142.2	90.0	139.8	246.0
Newfoundland	—	211.8	104.0	133.3	—	—	—
Borzoi	221.2	198.2	98.9	133.5	87.6	101.0	231.0
Doberman pinscher	214.4	190.4	95.1	122.1	81.4	112.5	210.0
Sheep-dog	234.0	188.1	94.0	122.2	—	111.8	221.1
Pointer	205.0	186.1	92.1	—	80.6	114.8	205.5
Setter	205.9	184.5	90.1	115.6	—	107.0	199.1
Dingo	192.6	169.3	86.3	109.2	74.7	101.0	187.5
Boxer	177.0	152.2	84.6	91.3	—	126.5	182.4
Poodle	181.8	160.0	83.8	104.9	70.7	101.6	185.5
Bulldog	161.5	138.8	81.6	82.8	—	117.1	155.0
Norweg. hare-dog	175.5	159.7	81.5	100.6	71.2	99.2	159.1
Schnauzer	171.5	155.0	80.0	—	68.8	98.8	153.9
Fox terrier	152.9	134.2	74.2	—	62.6	89.9	129.0
Whippet	136.8	123.4	72.1	80.5	57.6	78.2	134.2
Dachshund	142.5	122.6	69.3	83.1	—	82.9	90.5
Pekingese	90.2	79.2	60.3	41.2	39.7	77.0	95.3
Dwarf pinscher	97.0	84.1	59.0	57.2	—	64.9	83.5

(the former represented by the basal length and the latter by the length of the cranial cavity). The shorter the skull, the longer the cranial cavity.

In the wolf and the Irish wolfhound, the cranial cavity amounts to only 48.4 per cent of the skull length, while in dwarf dogs it increases to 76.3 per cent (Table VIII—Index 2); and in the Irish wolfhound and the King Charles spaniel of our examples, even to 45.6 per cent and 91.2 per cent, respectively (Table VI—Index 1). As the tables furthermore show, the specific race is irrelevant in this regard, only its size being pertinent. On the other hand, it can be demonstrated that the decrease of the body size does not alter the relation between the length of the skull itself and the length of the femur. In the Irish wolfhound as well as in the Pekingese, the femur shows about the same ratio, namely

97.3 and 94.7, respectively. In other words, the shortening of the femur is in direct proportion to that of the skull. Certain races, it is true, behave differently in this regard, as for instance the dachshund with a ratio of 157.3, but these apparently are specializations with no immediate bearing on our problem.

Two additional facts become apparent from Wagner's figures, namely the length-breadth relation of the cranium, and the relation between the length of the cranial cavity

TABLE VIII

INDICES OF THE MEASUREMENTS LISTED IN TABLE VII

	1 Total Length of the Skull and Length of the Femur $\frac{1 \times 100}{7}$	2 Basal Length and Endocranial Length $\frac{3 \times 100}{2}$	3 Endocranial Length and Length of the Face $\frac{4 \times 100}{3}$	4 Total Length of the Skull and Length of the Molar Row $\frac{1 \times 100}{3}$	5 Basal Length and Zygomatic Breadth $\frac{6 \times 100}{2}$	6 Length-Breadth Index of the Skulls after Wagner
Wolf	—	48.4	—	37.8	63.2	61.5
Irish wolfhound	97.3	48.4	139	—	54.1	47.3
St. Bernard	103.8	47.4	134	36.0	63.3	57.3
Newfoundland	—	49.2	128	—	—	56.0
Borzoi	95.7	49.8	135	39.7	50.6	56.0
Doberman pinscher	102.2	49.4	128	38.1	58.9	59.5
Sheep-dog	106.2	50.0	129	—	59.3	60.4
Pointer	100.0	49.4	—	39.3	61.7	62.6
Setter	103.5	48.9	128	—	57.9	62.1
Dingo	102.7	50.7	126	38.8	59.4	62.4
Boxer	97.0	55.5	108	—	83.0	68.5
Poodle	97.8	52.5	125	39.1	63.4	65.8
Bulldog	103.8	58.8	102	—	84.0	70.2
Norweg. hare-dog	111.2	51.1	123	40.6	62.1	66.5
Schnauzer	111.3	51.6	—	40.2	63.7	69.9
Fox terrier	118.4	55.2	—	40.8	67.1	69.8
Whippet	—	58.4	113	42.1	64.1	67.8
Dachshund	157.3	56.6	120	—	67.6	75.5
Pekingese	94.7	76.3	68.3	44.3	102.6	83.1
Dwarf pinscher	115.1	70.2	—	—	77.3	—

and the face. As illustrated by the three types (Figs. 1–5) there is a general tendency of the cranium to become brachycephalic corresponding to the decrease in size. The relative figures of the length-breadth indices, according to Wagner and listed in Table VIII, Index 6, are as follows: Irish wolfhound 47.3, bulldog 70.2, Pekingese 83.1 (in our three cases: 40.0, 69.5, 85.8). The increase of this index is mainly the consequence of the decrease of the cranium in length. Also due to this shortening is the length-reduction of the face. It appears still more pronounced if considered in relation to the length of the cranial cavity, for the latter is relatively longer in small-sized dogs (cf. above). Table VIII, Index 3,

shows that the index of the length of the cranial cavity and the length of the face decreases gradually from 139 (in large dogs) to 68.3 (in dwarf types).

Although Wagner did not overlook the fact that super-structures of the cranium are best developed in large dogs with strong masticatory apparatus, yet he failed to supply special measurements which could serve as indicators as to the degree of this development. He did, however, give a list recording the development of the frontal sinus. As already

TABLE IX

MEASUREMENTS AND INDICES OF THE SKULLS OF THE THREE DOG TYPES

I. Measurement	Irish Wolfhound ♂ (A.M.N.H. no. 90250)	English Bulldog (A.M.N.H. no. 69453)	King Charles Spaniel ♀ (A.M.N.H. no. 19182)
1. Total length (*op-pr*)	288	140.0	69.0
2. Basal length (*ba-pr*)	252	119.0	57.0
3. Length of the cranium	150	85.0	56.0
4. Endocranial length	115	76.0	52.0
5. Zygomatic breadth	130	112.0	58.0
6. Cranial breadth	60	59.0	48.0
7. Length of the face (*n-pr*)	151	63.0	5.0
8. Maxillo-alveolar length	138	73.5	32.8
9. Maxillo-alveolar breadth	80	62.5	38.3
Capacity in cc	145	80	55
II. Indices			
Endocranial—basal length $\frac{4 \times 100}{1}$	45.6	63.8	91.2
Cranial length-breadth index $\frac{6 \times 100}{3}$	40.0	69.5	85.8
Endocranial—facial length $\frac{4 \times 100}{7}$	131.0	83.0	9.6
Maxillo-alveolar index $\frac{9 \times 100}{8}$	58.0	84.9	116.6

mentioned above, this sinus corresponds to the anterior elevation of the cranium behind the postorbital process (Fig. 2, *C*), particularly well pronounced in large dogs. Fig. 7 illustrates the location and extension of the sinus (*fs*) with regard to the cranial cavity and the olfactory recess (*or*), on one hand, and the postorbital process (*pp*), on the other. These air-sinuses are typical for super-structures of the cranium and, therefore, missing in all those cases lacking super-structures as in the dwarf dogs with relatively large cranial cavities and small masticatory apparatus. Wagner estimated the presence and absence of the sinus and the degree of its development merely on the basis of the degree of the development of the anterior elevation behind the postorbital process (Fig. 7). Despite the questionable reliability of this method, Wagner feels justified in stating that this sinus

is well developed in large races and missing in dwarf types. Apart from the unreliability of the method, the presence or absence of the sinus depends to an appreciable extent upon the age of the individual. Nevertheless, Wagner's list is reliable in so far that it actually confirms his statement, namely the presence of the sinus in large dogs and its absence in dwarf types (Table X).

The shortening of the face, especially of the upper jaw, affects the form of the palate to an extraordinary extent (Fig. 6). The palate of the Irish wolfhound is long and narrow (*C*), while that of the King Charles spaniel (*A*) short and broad, and that of the English bulldog (*B*) leaning more towards the type of the spaniel than towards the former. The differences can best be illustrated by the maxillo-alveolar index of the three dogs which

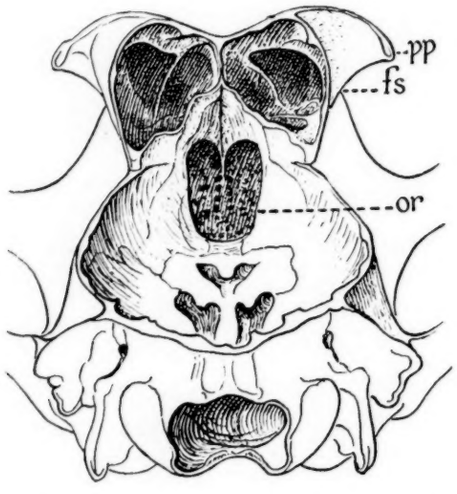

FIG. 7. Skull of an adult male dingo. Coll. A.M.N.H. no. 65847. 3/4. Viewed from above and behind. The cranial cavity has been opened so as to expose its anterior end and its topographical relation to the frontal sinus (*fs*). Abbrevations: *pp*, postorbital process; *or*, olfactory recess.

amounts to 58.0 in the wolfhound, 116.6 in the spaniel and 84.9 in the bulldog. This implies that the length of the palate in the spaniel is just one half of that of the wolfhound, while the breadth remains unchanged. The first consequence of this shortening is the remarkable restriction of space occupied by the teeth. The gaps between the teeth become less (Fig. 6, *B*) and the premolars and molars shift their direction from a sagittal to a transversal position. In addition, there is a strong tendency for the anterior premolars to become vestigial teeth and the third molars entirely lost.

Two other rather characteristic phenomena go hand-in-hand with the shortening of the face and the relative expansion of the brain case. In large types such as illustrated in Fig. 1 (*C*), the entire set of teeth is situated completely in front of the anterior end of the cranial cavity, the first molar even being considerably before the medial margin of the orbit. The degree of extension of the molar row and its typographical relation to the cranium and the cranial cavity is indicated by two vertical interrupted lines in Fig. 4 (*C*). In dwarf types (*A*) the whole set of teeth has shifted considerably towards the rear with the molar row now underlying the entire orbital and frontal portion of the cranial cavity

(Fig. 4, *A*). The bulldog (Figs. 1 and 4, *B*) exhibits an intermediary position also in this respect, the molar row still being situated in front of the anterior end of the cranial cavity but much closer to it than is true in the wolfhound (*C*).

The other phenomenon concerns the direction taken by the muzzle. As already mentioned above, there is the trend in the dwarf dog not only to reduce the face in longitudinal direction but also in height. In orientating the skulls in suborbital-porion plane, the upper jaw of the wolfhound (Figs. 1 and 4, *C*) will be found to be directed not only forward but also downward, whereas in the spaniel (*A*) the direction of the jaw is horizontal, and that of the bulldog (*B*) again intermediary. In extreme cases like the Pekingese or the King Charles spaniel, this increasing transformation of the face brings about a real inter-

TABLE X

Occurrence of Frontal Sinus in Dogs (After K. Wagner, 1930)

	Missing	Faint	Developed	Pronounced
Wolf	—	—	5	6
St. Bernard	—	—	2	—
Borzoi	1	—	—	—
Doberman pinscher	1	—	1	1
Sheep-dog	—	—	6	1
Pointer	—	—	3	5
Setter	—	—	10	5
Dingo	—	—	4	1
Boxer	7	7	1	—
Poodle	—	1	—	1
Bulldog	3	1	—	—
Norweg. hare-dog	3	6	1	—
Schnauzer	2	2	—	—
Fox terrier	4	2	—	—
Dachshund	1	—	1	—
Pekingese	2	—	—	—
Dwarf pinscher	2	—	—	—

ruption in the plane of the alveolar process of the jaw, with the anterior part up to the carnassial extending upward steeply, while the tooth itself together with the molars retains its original position. This lifting of the incisor and canine region in dwarf jaws produces a deep curve on the outline of the nasal and frontal region which becomes still more accentuated by the extreme bulging of the latter region. In large dogs, there is only a slight depression within the nasal area. Breeders of dogs call this characteristic concavity "stop." As Fig. 1, *A*, shows, it completely corresponds in location and degree to the interruption on the plane of the alveolar process within the molar region. The English bulldog (*B*) fails to show such a stop, despite the considerable shortening of the jaw. Nevertheless, the lifting of the anterior portion of the alveolar process is already indicated.

The lower jaw of dwarf dogs is also adapted to the changed conditions. In large types, the mandible represents a straight bone which completely harmonizes in length with the upper jaw. In dwarfs, however, the bone is not only shortened but at the same time becomes more and more curved, thus assuming the shape of a "rocking" mandible as this

form is called in man. Since in extreme cases, this transformation is not sufficient as to fully compensate the shortening of the upper jaw, the mandible is undershot.

It is self-evident that a decrease in size of the skull and shortening of the muzzle must also affect the teeth. First, it is to be expected that all the teeth of dwarf dogs are reduced in size, crowns as well as roots. As an example of that reduction, measurements of length and breadth of the first and second upper molars of the Irish wolfhound and the King Charles spaniel are given below:

	First Upper Molar		Second Upper Molar	
	Wolfhound	Spaniel	Wolfhound	Spaniel
Greatest length	14.8	5.9	9.6	2.8
Greatest breadth	20.0	7.2	14.1	4.8

The fact that this reduction is proceeding proportionately to the shortening of the skull can be gathered from the index figures of Table VIII (Index 4). In all large and medium-sized dogs, the length of the molar row amounts to 36.0 to 39.7 per cent of the total length of the skulls; in dwarf dogs the percentage is somewhat higher, reaching 44.3 per cent in the Pekingese which means that the molars in this case are slightly longer than the size of the skull infers. In many instances, however, the reduction of the teeth has advanced to such an extent as to cause the third molar or one of the premolars to become lost. In the case of the King Charles spaniel given as an example, the third molar is absent. Wagner (1930) records the percentage of the absence of premolars and molars in his material as follows:

TABLE XI

Absence of Premolars or Molars Observed by K. Wagner (1930)

0– 1%	St. Bernard, setter, dingo, grayhound, pointer, sheep-dog
1– 4%	Newfoundland, schnauzer, dachshund, German shepherd dog, poodle, borzoi, Norweg. hare-dog, large whippet, bulldog, Doberman pinscher, fox terrier
4– 8%	Boxer, French bulldog, small whippet
10–16%	Pug, dwarf pinscher, Bolognese

In regard to the Pekingese, Wagner experienced difficulties in determining whether the teeth had been shed later or were primarily absent. In any case, Wagner's list proves incontestably that there is a growing tendency for the molars to become lost the nearer the races approach dwarf types. Hilzheimer (1906) who also found that teeth were frequently missing in dwarf races came to a similar result. Although this author doubts that the shortening of the jaws may directly be responsible for the deficiency in the dentition, he nevertheless admits that the enormous transformation of the entire body may be the underlying cause.

Not less important than the reduction and loss of teeth is the appreciable alteration of their forms and pattern concomitant to the decrease in size. This is particularly true of the premolars and molars, both upper and lower. To begin with the upper molars (Fig. 8), in the first molar of the Irish wolfhound ($A : M^1$) the paracone is the strongest and

highest cusp followed by the metacone. In addition, there are two tiny accessory cusps, a protoconule and a metaconule. The cingulum has a distinctly developed hypocone, parastyle and metastyle being present. As to the loph formations the lingual ends of the proto- and metaloph are developed. The second molar (A: M^2) is considerably smaller than the first and differs therefrom in that all the details just mentioned are less pronounced. The paracone is reduced to the size of the metacone and the metacone almost completely lost, while the protoconule is still recognizable. The hypocone has lost its top and appears only as a special swelling of the cingulum.

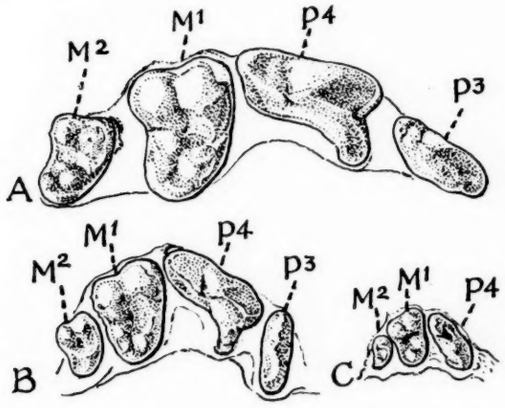

FIG. 8. Right upper premolars and molars of the three dogs of Fig. 1. Occlusal view. 1/1. *A*. P^3, P^4, M^1, M^2 of the Irish wolfhound. *B*. P^3, P^4, M^1, M^2 of the English bulldog. *C*. P^4, M^1, M^2 of the King Charles spaniel.

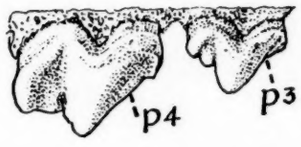

FIG. 9. Right upper premolars (P^3, P^4) of the Irish wolfhound. Buccal side. 1/1.

The first molar (M^1) of the King Charles spaniel (*C*) is not only remarkably smaller than that in the Irish wolfhound but also entirely changed in pattern characteristics. Paracone and metacone as such, it is true, are still rather distinct but more pointed. The protocone has merged into the cingulum. Hypocone and protoconule are considerably reduced and likewise the loph formations. The cingulum has disappeared, except in the hypocone, para- and metastyle regions. In the second molar (M^2) the reduction in size and pattern is complete with only the paracone retained, while the protocone and metacone remain merely as slight elevations of the cingulum.

The first molar (M^1) of the English bulldog (*B*) shows, apart from the reduction in size, no essential differences when compared with the wolfhound. Only the protoconule has disappeared and the metaconule becomes considerably smaller. The cingulum is less pronounced and the tooth without any traces of loph formations. In the second molar (M^2) paracone, metacone and protocone are still present, while hypocone, protoconule,

metaconule and the loph formations have disappeared in addition to the cingulum being considerably reduced.

The fourth premolar—carnassial tooth—(Figs. 8 and 9, P^4) in the wolfhound (*A*) shows the cingulum to be especially developed on the mesial and lingual sides. The protocone [1] looks more like a localized and pointed portion of the cingulum with which also the parastyle is united. The metastyle shear is divided by a faint indentation. In the third and second premolars, the parastyle is missing and the metastyle distinctly divided into two cusps (Fig. 9). The protocone appears reduced to a style-like edge which descends medially and lingually from the paracone. The cingulum is restricted to the lingual side. The first premolar displays only small elevations of the cingulum on its mesial and distal corners.

In the fourth premolar (P^4) of the King Charles spaniel (Fig. 8, *C*) the protocone is indicated only by a faint projection of the respective corner, while the parastyle is missing.

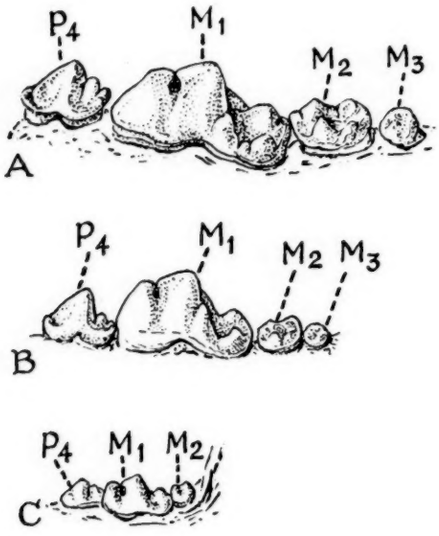

FIG. 10. Right lower premolars and molars of the three dogs of Fig. 1. Viewed from the occlusal and lingual side. 1/1. *A*. P_4–M_3 of the Irish wolfhound. *B*. P_4–M_3 of the English bulldog. *C*. P_4–M_2 of the King Charles spaniel.

The metastyle is a unitary blade. The cingulum is completely lacking. The third and second premolars are missing. The first premolar is represented by a tiny tooth with one cusp and faint elevations on the mesial and distal corners. In a Japanese dwarf spaniel at our disposal (Coll. A.M.N.H. no. 2548) the third premolar is present. The metastyle consists of a rather small cusp and the parastyle is merely indicated by a faint trace on the mesial corner. The second and the first premolars do not differ essentially from the corresponding teeth of the wolfhound, except that they are much smaller and the metastyles missing.

As to the English bulldog (Fig. 8, *B*) the fourth premolar has no parastyle, the metastyle being represented merely by a unitary blade. The cingulum is developed but not

[1] I am following Gregory and Hellman's (1934) nomenclature.

as distinct as in the wolfhound. The other premolars fail to show any appreciable alterations, with the exception of the considerable reduction in size.

These differences in large and small dogs are much more apparent in the lower premolars and molars (Fig. 10) than in the upper ones. In the first molar—carnassial tooth (M_1)—of the wolfhound (*A*) the protoconid is by far the dominating cusp, the paraconid appearing merely as the separating anterior portion of the blade which descends from the tip of the cusp towards the mesial corner of the crown, while the metaconid is represented only by a low and negligible appendix on the distal and lingual slope of the main cusp. The talonid is well developed, displaying three cusps, namely the hypoconid on the labial side, the smaller entoconid on the lingual side and a small accessory cusp between the latter and the metaconid. Its posterior end is formed by the cingulum. The second molar (M_2) is much smaller than the first one and seems to be represented chiefly by the talonid. The paraconid is missing. The protoconid is reduced to a low cusp, not much higher than the metaconid. Hypoconid and entoconid are present and the cingulum forms the mesial and distal rim of the crown. The third molar (M_3) is completely a rudimentary tooth with a low central double cusp, two small elevations before and a faint cingulum around it.

In the first molar of the King Charles spaniel (Fig. 10, *C*) the protoconid and the paraconid form the essential parts of the crown with the metaconid completely missing and the entire talonid diminished to one single cusp which may correspond to the hypoconid merging into the cingulum. The tooth looks more like a tricuspid premolar than a molar. The second molar (M_2) is wholly reduced and no longer shows any special details. It resembles the third molar of the wolfhound. The third molar is missing.

In the English bulldog (Fig. 10, *B*) the conditions are about the same as in the wolfhound as far as the first molar is concerned, only the cusps of the talonid are less pronounced and the accessory cusp lost. The second molar is already considerably reduced, although the cusps are still but just recognizable. The third molar is very small and displays but an indistinct elevation in the middle of the surface.

As to the lower premolars the differences between large and dwarf types are apart from the size not as marked as in the molars. In the wolfhound (Fig. 10, *A*) the cingulum is rather pronounced and forms a distinct but low cusp-like elevation on the mesial as well as on the distal edge. The fourth (P_4), third and second premolars show the same pattern and differ only in size. There is one main cusp and an accessory lower one on the distal side. In addition, the cingulum which is rather pronounced rises on both mesial and distal edge to low cusp-like elevations. A sharp blade descends from the tip of the main cusp to the cingulum elevation of the mesial edge. The markedly small first premolar consists only of one cusp with the preserved cingulum merely on the lingual side.

In the King Charles spaniel (*C*) the fourth and third premolars are considerably reduced, resembling the first premolar of the wolfhound. The accessory cusp is retained in the fourth but lost in the third tooth. The blade has lost its cutting character. The first premolar is rather small but does not differ from the corresponding tooth of the large types. The second premolar is missing.

The pattern of the fourth and third premolars (*B*) of the English bulldog is the same in principle as in the wolfhound but with all the special formations less pronounced. In the second premolar the accessory cusp is not developed. The first premolar is a vestigial tooth.

It follows from this description that the premolars and molars of the dwarf types, particularly the latter, have not merely become reduced in size such as to represent diminutive patterns of the large teeth but changed their entire character which may be defined in general as a simplification. The number of cusps becomes diminished and the cusps themselves become lowered and rounded; the cingulum and all the essential differentiations of the chewing surface show the tendency to disappear. Thus, the differences that do exist between the individual teeth of the large types, on one hand, and the dwarf types, on the other, are almost identical with those between the well developed and the more reduced teeth in one and the same large type; the first upper molar of the dwarf spaniel, for instance, resembles to a certain extent the second upper molar of the wolfhound. The entire modification thus appears as a direct result of the reduction in size of jaws and skull.

It has been shown that dwarfism in dogs brings about a rather marked transfiguration of all parts of the skull. Viewed from the morphological standpoint, the enlargement of the brain and the cranium proper at the expense of the remaining skull must be considered the decisive factor of such far-reaching transformations as to affect even the pattern of the teeth. Since there is a continuous line which leads from the largest types to the extreme

TABLE XII

SKULL MEASUREMENTS AND INDICES OF SOME WILD DOGS

Species	Measurements							Indices			
	1 Total Length of the Skull	2 Basal Length of the Skull (*ba-pr*)	3 Endo-cranial Length	4 Zygo-matic Breadth	5 Max.-Alveo-lar Length	6 Max.-Alveo-lar Breadth	7 Length of the Face (*n-pr*)	1 Basal and Endo-cranial Length $\frac{3 \times 100}{2}$	2 Basal Length and Zygo-matic Breadth $\frac{4 \times 100}{2}$	3 Max.-Alveo-lar Length and Breadth $\frac{6 \times 100}{5}$	4 Basal Length and Length of the Face $\frac{4 \times 100}{7}$
Canis lupus ♂ A.M.N.H. no. 34446	266	226	99	144	125	85	132	44.0	63.8	68.1	56.2
Canis lupus ♂ ♀ after Wagner (1929)	255	221	107	140	—	—	—	48.4	63.5	—	—
Chrysocyon? A.M.N.H. no. 12099	249	220	85	125	116	65	132	38.7	56.8	56.1	60.1
Thos adusta ♂ A.M.N.H. no. 83131	161	147	56	85	81.5	52	—	38.1	57.8	63.8	—
Thos mesomelas ♀ A.M.N.H. no. 27739	146.5	131	60	78	73	45	—	45.7	59.5	61.7	—
Thos adusta ♀ A.M.N.H. no. 27736	143	132	57	82	71	47.5	—	43.2	57.3	66.8	—
Vulpes vulpes hoole ♀ A.M.N.H. no. 10109	148	134.5	61	74	75	43	69	45.4	50.0	57.3	51.3
Vulpes vulpes hoole ♂ A.M.N.H. no. 44782	140	128	63	74	71.5	41.5	—	49.3	52.9	58.0	—
Pseudalopex gris. ♀ A.M.N.H. no. 69584	122	113	53	62.5	63	35	—	46.9	51.3	55.6	—
Fennecus zerda ♂ A.M.N.H. no. 90156	81	77	44	45	40	26	32	57.2	55.7	65.9	41.5

dwarfs with intermediary stages, the final effect cannot be taken as merely an incidental product of some special and eventually abnormal growth factors but must be counted as an instructive demonstration of nature to what extreme results the constantly driven trend to expand the cranial cavity leads. In how far this process is influenced by what we call domestication is of secondary significance and has no bearing on the morphological problem discussed herein. If we are really dealing with a general principle, we should expect to find the same conditions in large and small wild dogs as well as in other families or orders of mammals. It must be taken into account, however, that in the case of domesticated

TABLE XIII

SKULL MEASUREMENTS AND INDICES OF SOME FELIDAE

Species	Measurements							Indices			
	1 Basal Length of the Skull (*ba-pr*)	2 Endo-cranial Length	3 Cranial Ca-pacity in cc	4 Max.-Alveo-lar Length	5 Max.-Alveo-lar Breadth	6 Length of the Pre-molar Row	7 Length of the Face (*n-pr*)	1 Basal and Endo-cranial Length $\frac{2 \times 100}{1}$	2 Max.-Alveo-lar Length and Breadth $\frac{5 \times 100}{4}$	3 Pre-molar Row and Basal Length $\frac{6 \times 100}{1}$	4 Basal Length and Length of the Face $\frac{7 \times 100}{1}$
Felis leo massaica ♂											
A.M.N.H. no. 30242....	294	114	230	136	135	72	159	38.8	99.5	24.5	61.6
Felis concol. aszeca ♂											
A.M.N.H. no. 1330.....	174.5	91	155	74	87.5	46	—	52.2	118	26.4	—
Felis concol. aszeca ♀											
A.M.N.H. no. 1339.....	146	83	145	61	75	39	—	56.7	123	26.7	—
Lynx canad. ♂											
A.M.N.H. no. 29036....	106	69	—	44	57	29	—	65.1	129	27.3	—
Lynx canad. ♀											
A.M.N.H. no. 22778...	103.5	70	85	42	56	27	47.5	67.7	133	26.1	44.9
Felis bengalensis sin. ♂											
A.M.N.H. no. 60054....	77	50	35	31	38.5	17	31.0	64.9	124	22.1	40.3
Felis bengalensis sin. ♀											
A.M.N.H. no. 60093....	71	50	25	28	35	16	—	70.3	125	22.5	—
Felis domestica ♂											
A.M.N.H. no. 22818....	78	50	25	31	39	20	—	64.2	126	25.7	—

dogs all variations in size belong to one and the same species, while in wild dogs large and small types represent genuinely different species. The same is true of other groups of mammals. The production of dwarfs or at least of types differing greatly in size seems possible only in exceptional cases within the same species. As this is not the place to enter into a discussion as to how far such discriminations depend upon the definition of "species," we shall return to this question elsewhere.

Table XII contains skull measurements and indices of certain representatives of wild dogs of different sizes as far as they have a bearing on the problem under discussion. It is apparent from these indices that the disproportion between the size of the body or skull and the size of the brain is less pronounced in wild dogs than in domesticated animals.

The differences between large and small types in this respect are not as marked, nor is there any graduation corresponding to the decrease in size. The fennec, the smallest type of all wild dogs, is the only exception as far as the relation between cranial cavity and basal length of the skull is concerned. This cavity is relatively larger than that in the wolf but not more than nine index units, while the differences between the Irish wolfhound and the King Charles spaniel amounts to 45 units (cf. Tables VIII and IX). Corresponding therewith is only a slight shortening of the face (Table VIII, Index 3). In the fox as well as in the fennec the jaws remain long and narrow like those of the wolf, neither is there any reduction in number of teeth nor any appreciable change in the character of the tooth

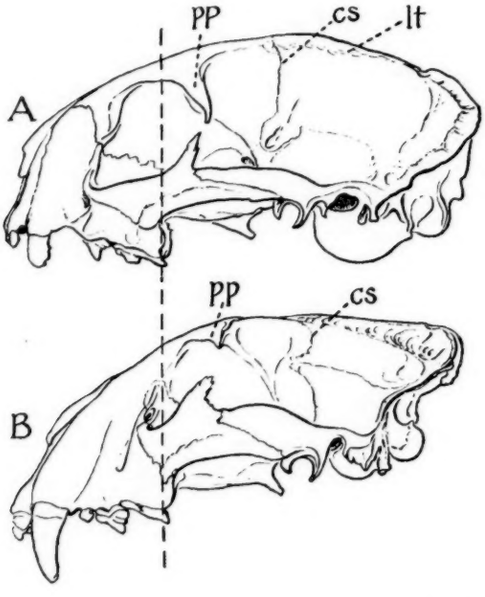

FIG. 11. Skulls of a wild cat and a lion, the latter reduced to the total length of the former. Lateral view. *A*. Adult male *Felis bengalensis sinensis*. Coll. A.M.N.H. no. 60054. 3/4. *B*. Adult male *Felis leo massaica*. Coll. A.M.N.H. no. 30242. About 1/5. Abbreviations: *cs*, coronal suture; *pp*, postorbital process; *lt*, temporal line.

pattern. The only difference between wolf and fennec in this respect is the occurrence of a metastyle in the second and third upper premolars and a metaconid in the third and fourth lower premolars in the wolf, while both features are not developed in the fennec.

Dwarf wild dogs, in contrast to the domesticated dog, are diminutive forms of the large types. Their cranial cavities are only slightly larger than implied by the size of their skulls and bodies. The same holds good for the brain itself as will be shown later. There is, however, one peculiarity in which the smaller types of wild dogs approach the corresponding types of the domesticated forms, namely in the formation of the super-structures of the cranium. In the large types the sagittal and nuchal crests are well developed; the protuberance between the postorbital process and the coronal suture which lodges the frontal sinus is likewise rather pronounced. In the small types, there is no sagittal crest, while the nuchal crest is weak and the temporal lines reach the middle of the cranium only

within the lambda region. In fennec as well as in fox the frontal sinus is lacking. These peculiarities apparently are due to the fact that the entire masticatory apparatus is less developed in these forms than in the large ones (cf. below).

It is of special interest to note that as regards the differences between large and small types, Felidae deviate from the wild Canidae in behaving like domesticated dogs. Table XIII gives the measurements and indices of some representatives of the Felidae group differing in size.

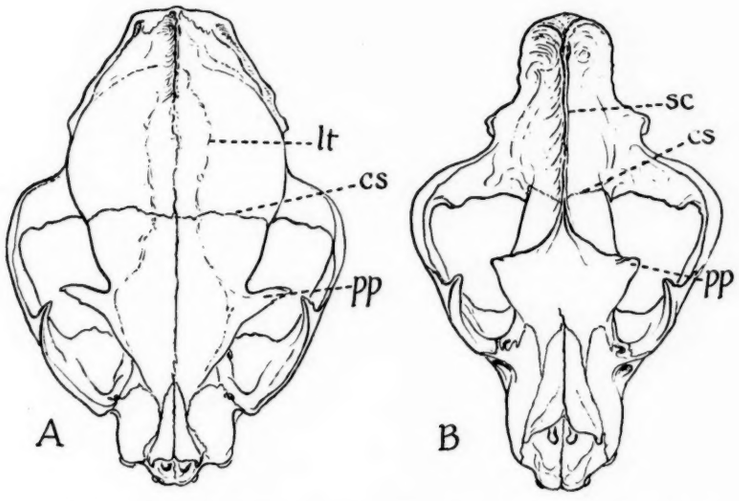

FIG. 12. The same skulls as in Fig. 11 in vertical view. Abbreviations: *sc*, sagittal crest; *lt*, temporal crest.

In Figs. 11–12 the skull (*B*) of an adult male lion (*Felis leo massaica*, Coll. A.M.N.H. no. 30242) is compared with the skull (*A*) of an adult male wild cat (*Felis bengalensis sinensis*, Coll. A.M.N.H. no. 60054), the former being reduced to the same total length of the latter. The differences are obvious. The cranium of the lion (Figs. 11 and 12, *B*) is long and narrow, with the super-structures well developed. The postorbital processes (*pp*) are very heavy and continue backward into a high sagittal crest (*sc*). This terminates into a large pyramid-shaped projection of about 50 mm in height in which the nuchal crest merges. The space between coronal suture (*cs*) and postorbital process is occupied by a special swelling which is somewhat separated from the posterior part of the cranium and lodges the frontal sinus. The length of the cranial cavity amounts to only 38.8 per cent of the total length of the skull. The face corresponding to the form of the cranium is likewise long and relatively narrow.

In the wild cat (Figs. 11 and 12, *A*) the cranium is short with the brain case proper forming a wide ovoid. The super-structures are reduced to a small sagittal crest restricted to the lambda region where it joins a well developed nuchal crest to form a low and broad pyramid-like projection. The postorbital process (*pp*) is flat and gives origin to a distinct temporal line (*lt*) which courses in some distance from the midline backwards toward the lambda region to continue there into the sagittal crest and occipital pyramid. The space between coronal suture (*cs*) and postorbital process (*pp*) appears even when viewed from the outside as a part of the brain case itself. There is no frontal sinus, the cranial cavity

extending up to the postorbital process. In accordance therewith, the length of the cavity amounts to 64.9 per cent—in female individuals of the same species even to 70.3 per cent—of the total length of the skull. As the lateral view (Fig. 11) reveals, the entire skull of the wild cat is relatively not only much broader but also higher than the lion skull. In correlation to the extension of the cranial cavity the face of the cat skull is considerably shortened when compared with that of the lion but at the same time broader and higher. The length of the face amounts to 61.6 per cent of the basal length of the skull of the lion but only to 40.3 per cent in the cat.

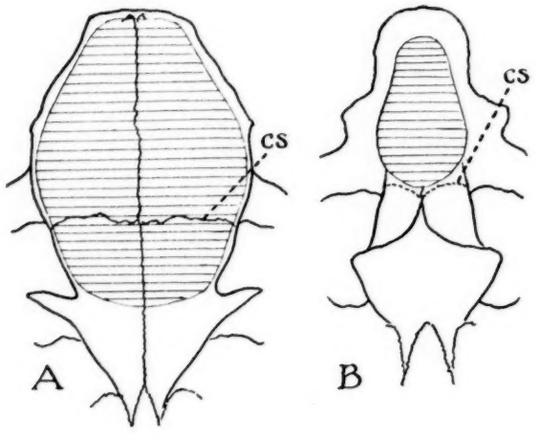

FIG. 13. Outlines of the same skulls as in Fig. 12, showing comparative dimensions of the cranial cavities (shaded) of the small and large types. Abbreviation: *cs*, coronal suture.

Figure 13 illustrates the topographical relation of the cranial cavity to cranium and face. In the lion (*B*) the anterior pole of the cavity does not reach the coronal suture while in the cat (*A*) it extends far beyond this mark and occupies the posterior moiety of the entire frontal region. This forward extension, together with the considerable widening of the cavity in lateral direction, has the same effect upon the walls of the brain case as outlined above for dwarf dogs. The thickness of the parietal bone is only 0.5 mm in the cat against 4.0 mm in the lion. Furthermore, the metopic suture is preserved in the cat in the adult stage (Fig. 12, *A*), while it is obliterated in the adult lion (Fig. 12, *B*).

The shortening of the face of the cat and the extension of the cranial cavity yielded a similar effect upon the relative position of the alveolar process of the upper jaw as observed in dwarf dogs. In the lion (Fig. 11, *B*) the level of the carnassial and rudimentary first molar falls almost before the origin of the zygomatic arch and the entrance of the orbit (cf. dashed vertical line in Fig. 11), whereas in cat (*A*) this vertical line cuts the arch and the orbit much more towards the rear. Furthermore, in the lion the muzzle not only extends forward but also downward if the skulls are orientated in the suborbital-porion plane, while in the cat the muzzle as a whole remains in the same plane with the incisor-canine region even slightly lifted. Both phenomena are characteristics of dwarf dogs (see above) with the only difference that they are much more pronounced there than in the cat.

Notwithstanding these similarities between dogs and cats, there is one important difference. In large dogs the palate and the dental arch are long and narrow, but short and wide in dwarf dogs (cf. Fig. 6). This does not apply to the cat. In small wild or domesticated cats the palate is relatively broader, it is true, than in the lion, the maxillo-alveolar index amounting to 126 in the former against 99.5 in the latter, but the lion already shows a rather high index, especially when compared with the wolf or the wolfhound in which this index declines to 68.4 and 58.0, respectively (against 116.6 in the King Charles spaniel). An explanation for such divergency may, I believe, be found in the behavior of the dentition. In all cats, large and small, the molars and partly also the premolars are either missing or rudimentary. In the upper jaw the first premolar is absent and the second rudimentary; only the third and fourth are well developed teeth. Of the molars the first one is rudimentary and the second and the third are completely missing. The premolars of the lower jaw show the same conditions as exist in the upper one, while the first molar changes into the carnassial tooth and the two following ones disappear. The Felidae as an entire group, therefore, must have once experienced an immense reduction in face. Gregory and Hellman (1939) state that a genetta-like Viverridae type probably represents the ancestral form from which the Felidae took origin. Genetta is equipped with all four premolars and the first and second molars. Corresponding thereto, its face

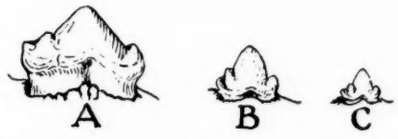

FIG. 14. Lower third premolars of lion, lynx and wild cat. Buccal view. 1/1. *A. Felis leo massaica*, male. Coll. A.M.N.H. no. 30242. *B. Lynx canadensis*, male. Coll. A.M.N.H. no. 29036. *C. Felis bengalensis sinensis*, male. Coll. A.M.N.H. no. 60054.

and palate are long and narrow with the maxillo-alveolar index amounting to 67.4 (*Genetta servalina* ♂ Coll. A.M.N.H. 51571: alveolar length 38.7 mm, alveolar breadth 26.4 mm). This implies that the Felidae primarily were small animals with a tendency to produce such large types as lion and tiger. But in spite of the considerable enlargement of the body, together with all the consequences on the special formation of the skull, the reduction of the dentition could not be reversed and the dental arch thus retained its primarily acquired shape.

This fixation may also be responsible for such insignificant differences of tooth pattern between large and small types of the Felidae group. In the small types the premolars and molars, of course, are considerably reduced in size when compared with the same teeth of the large group. But as is evident from Fig. 14, the pattern proper remains unchanged. The only alteration concerns the form. The lower third premolar in the lion (*A*), for instance, exhibits a rather heavy crown with a low, broad and thick major cusp, while the crown of the cat (*C*) is very fine with a high, narrow and thin cusp. These differences are best illustrated by the length-height index of the crown which is 62.6 in the lion against 80.1 in the domesticated cat.

With regard to forms intermediary between large and small types, there is as a whole a fairly exact gradation in correspondence to size. As Table XIII reveals, the females show the characteristic correlations of small types slightly more pronounced than males.

It is not intended herein to include a scrutiny of all the groups of mammals for the purpose of determining whether and to what extent the correlations under discussion had come into effect in individual orders. Yet the primates present a proper touchstone for the verification of the general validity of any law which may underlie the transformations of the skull concomitant to differences in body size. A rather instructive example can be found in Platyrrhinae, on one hand, and the Cercopithecinae and anthropoids, on the other. It is well known—I shall return to this question later—that the group of marmosets, despite the smallness of their body, have a very large brain (cf. Table II). The length of the cranial cavity, for instance, in *Saimiris* amounts to 82.3 per cent of the total length of the skull measured from opisthocranion to prosthion, while this index declines in the large-sized anthropoids as, for instance, in male gorilla to about 51 per cent and in male chimpanzee to about 38 per cent. Even if we confine ourselves to one and the same group, the differences show no tendency of becoming smaller as evident from the measurements and indices of a *Saimiris* and an *Alouatta* in Table XIV. The howler, it is true, is

TABLE XIV

MEASUREMENTS AND INDICES OF SKULLS OF A SMALL AND A LARGE TYPE OF PLATYRRHINE MONKEY

Species	Measurements					Indices	
	1 Total Length of the Skull (*op-pr*)	2 Endocranial Length	3 Cranial Capacity in cc	4 Max.-Alveolar Length	5 Max.-Alveolar Breadth	1 Total Length of the Skull and Endocranial Length $\frac{2 \times 100}{1}$	2 Max.-Alveolar Breadth and Max.-Alv. Length $\frac{5 \times 100}{4}$
Saimiris sciurea ♂							
A.M.N.H. no. 33875	66.4	55.2	27	18.7	20.5	82.3	109.6
Alouatta senicula ♂							
A.M.N.H. no. 69591	123.0	67.0	65	47.1	43.3	54.4	92.2

a particularly specialized form (cf. Leche, 1912) and its specialization to a certain extent affects the form of the face and the position of the upper jaw; nevertheless, when compared with a marmoset, it represents the large type of a platyrrhine, thus exhibiting most of the features characterizing such a type. Fig. 15 shows the skull of an adult male howler (*B*) in lateral view. The cranium is heavy, long and relatively low. The parietal bone is 1.3 mm thick; the sutures are obliterated. There is no real forehead; the face extends directly forward in continuation of the length axis of the cranium. The super-structures are well developed and consist of distinct supra-orbitals separated from the cranium by a slight depression, the sagittal crest rises from the lambda region and merges into a pronounced nuchal crest. The upper jaw is extremely long and high with the molars entirely in front of the orbit. The skull of an adult *Saimiris* (*A*), on the other hand, displays all the peculiarities of a dwarf type. The cranium is considerably enlarged in all dimensions and extremely frail, the parietal bone being only 0.6 mm thick; the sutures are patent. There is a distinct and well vaulted forehead, while all the super-structures are completely

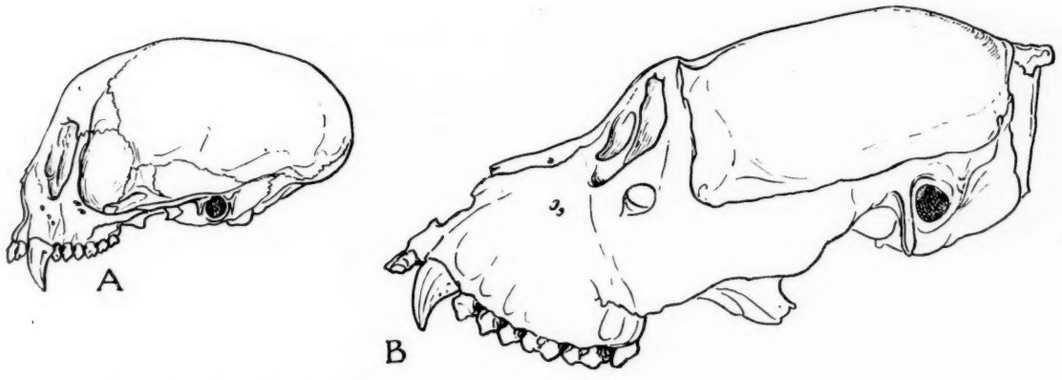

FIG. 15. Skulls of small and large types of platyrrhine monkeys. Lateral view. 3/4.
A. Saimiris sciurea, male. *B. Alouatta senicula*, male.

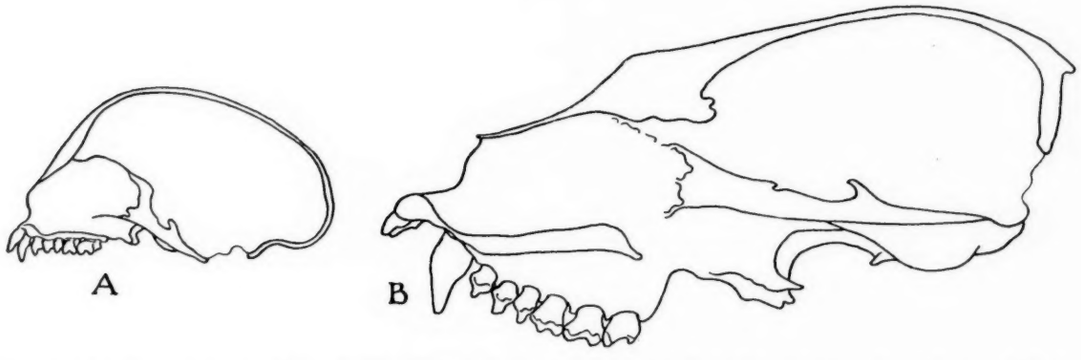

FIG. 16. Median sections through the skulls of an adult female *Saimiris sciurea*, *A*, and an adult male *Alouatta ursina*, *B*. After Leche (1912). 3/4.

lacking. The face, extremely short and low, has shifted backwards and almost underlies the frontal portion of the cranium. The molars compared to those of the howler are short and high and their pattern appears more simplified. A median section through both skulls (Fig. 16) reveals the characteristic differences between the size and the topographical relations of the cranial cavities and the facial parts. The cranial cavity of the howler (*B*) is long and low and located entirely behind the nasal cavity; the foramen magnum occupies the posterior end and opens in backward direction. In *Saimiris* the cranial cavity is relatively much higher and with its anterior portion directly superposed upon the nasal cavity. The foramen magnum is located near the middle of the base and opens almost completely downward. The facial parts are relatively much smaller in *Saimiris* than in the howler. The frontal sinus is lacking in *Saimiris*. Such, however, is also the case in *Alouatta*, though the anterior wall of the brain case is considerably thickened.

Saimiris and *Alouatta* represent, it is true, two different genera or families of the platyrrhine group but their conditions correspond entirely to those characteristic of dwarfs and large types. That, however, also in one and the same species of the platyrrhine group form and size of forehead and face can be closely correlated is revealed by the variations

in the development of the forehead of the Spider monkey, reported by Adolph H. Schultz (1926 b). Cases in which one could speak of a real forehead such as is understood when applied to man are not rare. Fig. 17 illustrates the two extreme examples observed by Schultz: *B* represents the more common type with a low retreating forehead and pronounced supra-orbitals separated from the former by a distinct furrow. *A*, on the other hand,

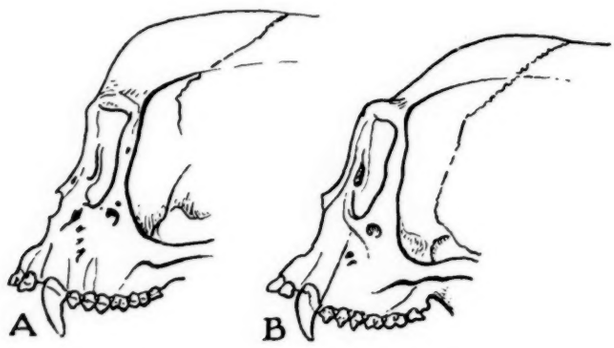

FIG. 17. Skulls of two adult male *Ateles Geoffroyi*, after A. H. Schultz (1926). Lateral view.

shows the type with a high and well vaulted forehead and rather weak supra-orbitals in direct connection with it. These differences as pointed out by Schultz do not constitute the only ones. The entire face of type *B* is larger, heavier and much more prognathous than is true in type *A*. According to Schultz the two monkeys are fully developed male individuals of approximately the same age. Suspecting that there may be differences also in the size of the skulls and cranial cavities, I approached Dr. Schultz for the measurements which he very kindly supplied and which are listed in Table XV. Unfortunately, neither body weight nor measurements of the skeletal parts could be taken. From the measure-

TABLE XV

TWO EXTREME TYPES OF *Ateles Geoffroyi* ♂, AFTER A. H. SCHULTZ

	Type A (No. 753)	Type B (No. 727)
Total length (*op-pr*)	106 mm	112 mm
Cranial length (*g-p*)	83 mm	87 mm
Endocranial length	74 mm	78 mm
Cranial capacity	89 cc	105 cc

ments of the skulls listed in Table XV it can only be surmised that in this instance the roominess of the cranial cavity of type *A* is in direct proportion to the size of the whole skull and not relatively larger as is the case in dwarf types.

An excellent example, however, illustrating the characteristic differences in morphological features of the skulls of dwarfs within the anthropoid groups is represented by the pigmy chimpanzee (*Pan paniscus*) and the ordinary form (*Pan schweinfurthi*). The race of the pigmy chimpanzee was first described by Ernst Schwarz (1929). Since then several additional specimens have become known. For the entire literature and details the reader

is referred to Harold J. Coolidge's paper (1933) which contains also some interesting photographs of the skull. I was given the opportunity to study the skull of an adult pregnant female (no. 86857, Coll. A.M.N.H., collected by J. P. Chapin in 1930), the skull of a young male individual named "Prince Chim" by Robert M. Yerkes and likewise in the possession of the Museum (A.M.N.H. no. 54336), and finally the skull of an infant male specimen (A.M.N.H. no. 86855 also collected by J. P. Chapin). The total body height (crown to sole) of the first mentioned female individual amounted to 1010 mm, the length of the head and trunk (to tip of coccyx) to 630 mm. The measurements listed in Table XVI clearly show the essential differences between this female pigmy and an adult type of *Pan schweinfurthi* (Coll. A.M.N.H. no. 90191) of the same sex. The differences become still more apparent when the main views of the two skulls are compared as in Figs. 18–20. That the pigmy chimpanzee of Chapin's collection (no. 86857) must be considered a genuine

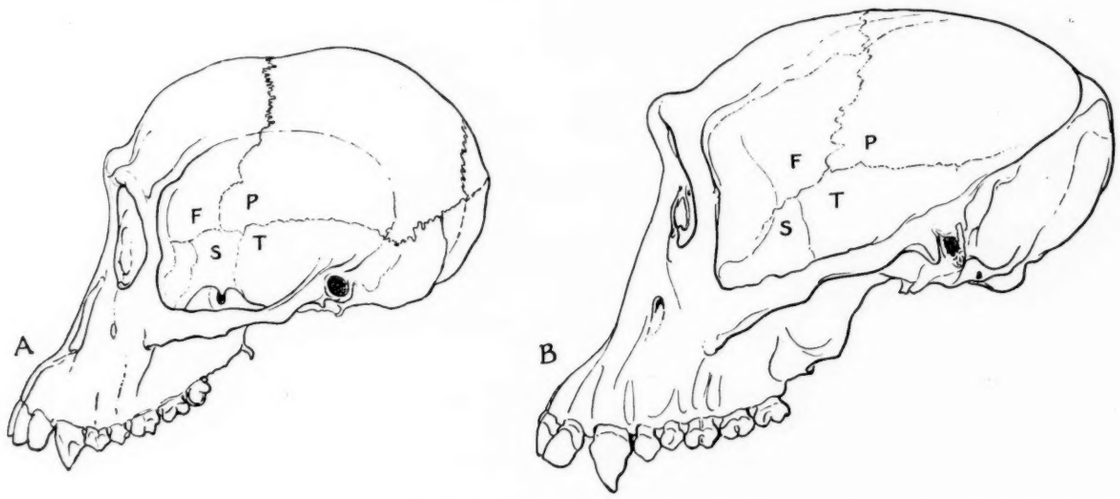

FIG. 18. Skulls of two adult types of chimpanzee. Lateral view. 1/2. *A*. Pigmy chimpanzee (*Pan paniscus*), female. Coll. A.M.N.H. no. 86857. *B*. Normal-sized type of chimpanzee (*Pan schweinfurthi*), female. Coll. A.M.N.H. no. 90191. Abbreviations: *F*, frontal; *P*, parietal; *S*, sphenoid; *T*, temporal.

dwarf and not merely a juvenile individual of the normal type can be deduced not as much from the fact that the animal had been pregnant—pregnancy is known to occur also in not fully mature individuals—but rather from the third molars in both upper and lower jaws being fully erupted and even partly worn and, in correspondence thereto, from the complete obliteration of the spheno-occipital suture.

When compared with the normal type of chimpanzee (Figs. 18–20, *B*) of the same sex and approximately the same age, the skull of the dwarf type (*A*) is much smaller as a whole. Notwithstanding this smallness, the brain case itself constitutes the major portion of the skull, while the face and especially the upper jaw appear to be reduced to a relatively much greater proportion than the cranium. This follows directly from the relation of the length of the cranial cavity to the total length of the skull which amounts to 65.4 per cent in the pigmy but only to 57.0 per cent in the normal type. The cranial capacity as such is, of course, smaller in the dwarf (cf. Table XVI); yet, since the body weight of the pigmy was

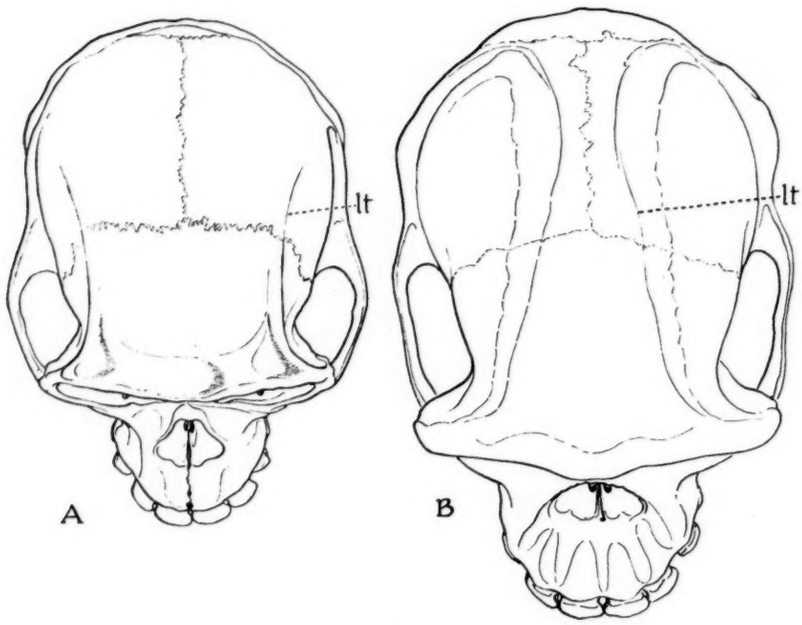

FIG. 19. The same skulls as in Fig. 18 in vertical view. 1/2. Abbreviation: *lt*, temporal line.

not recorded, it is not possible to calculate the actual relationship between size of the brain and that of the body. However, it may be reasonably assumed that this ratio is greater in the pigmy in correspondence to the rule governing all dwarf types.

The relatively greater size of the brain case of the pigmy skull infers the same as in the case of the skulls of dwarf dogs described above. The cranium, as a whole, is rounded off, that is to say, higher and broader than the typical form, the length-breadth indices amounting to 83.8 and 76.8, respectively, against 79.8 and 72.1 in the normal type, and the length-height index to 54.9 against 45.8. When viewed from behind (Fig. 20), the

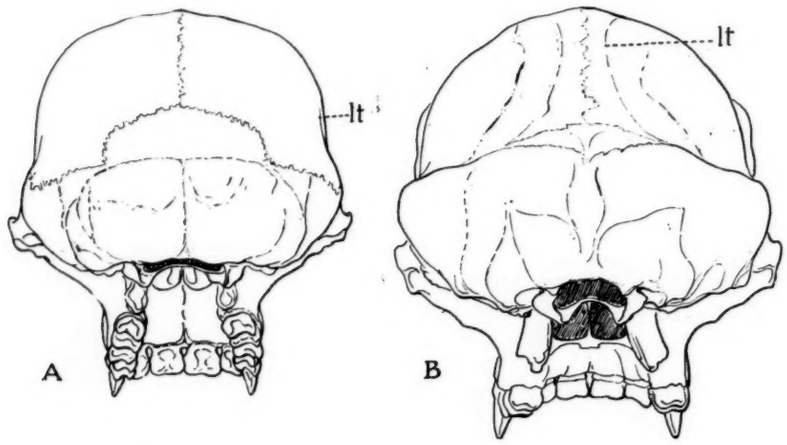

FIG. 20. The same skulls as in Fig. 18 in occipital view. 1/2. Abbreviation: *lt*, temporal line.

outline of the dwarf skull is distinctly seen to bend outward above the squamosal suture, while the normal type fails to show such a bulging; in other words, the dwarf skull displays in contrast to the normal type a typical parietal tuber. The conditions of the occiput reveal similar differences; in the normal type the occiput is elongated backwards, while in the pigmy it is more rounded off. The more globular character of the skull form is also evident in the location of the foramen magnum. As Fig. 20 illustrates, the foramen

TABLE XVI

MEASUREMENTS AND INDICES OF THE SKULLS OF AN ADULT FEMALE PIGMY CHIMPANZEE AND A NORMAL-SIZED SPECIMEN OF THE SAME SEX

A. Measurements (in mm)

	Pan paniscus ♀ (A.M.N.H. no. 86857)	*Pan schweinfurthi* ♀ (A.M.N.H. no. 90191)
Length of the femur	257	296
Total length of the skull (*op-pr*)	151	186
Basal length (*ba-pr*)	99	128
Endocranial length	98.5	106
Cranial capacity in cc	272 (Coolidge)	360
Greatest length of the cranium (*g-op*)	112	133
Greatest breadth of the cranium:		
a. Biauricular	94	106
b. On the plane of the squamosal suture	86	96
Auricular height	61.5	61
Distance of the lin. temp. sup. (chord):		
a. Middle of the frontal bone	47	40
b. At the coronal suture	51	29.5
c. Middle of the parietal bone	71	15.5
Maxillo-alveolar length	52	72
Maxillo-alveolar breadth	46	58.5
Length of the palate	48	68.5
Breadth of the palate	21.5	27.5
Length of the mandible (Incision—middle of the bicondylar breadth)	86	119
Bicondylar breadth of the mandible	86.5	100
Length of the premolar-molar row:		
a. Maxilla	39	50
b. Mandible	44	51
B. Indices		
Endocranial length to total length of the skull	65.4	57.0
Length-breadth index:		
(*a*)	83.8	79.8
(*b*)	76.8	72.1
Length-height index	54.9	45.8
Maxillo-alveolar index	88.5	81.3
Length-breadth index of the palate	44.8	40.2
C. Angles		
Facial angle	62°	60°

magnum in the pigmy skull occupies a more central position and opens distinctly less backwards and more downwards than in the normal type. Corresponding to this difference in the whole form, the pigmy skull shows the forehead to be high and well vaulted (Figs. 18 and 19, *A*) and the supra-orbitals only faintly developed, whereas in the normal type (Figs. 18 and 19, *B*) the forehead is flat and strongly receding and the supra-orbitals heavy and of considerable extension in forward as well as in lateral direction. The difference between the extension of the supra-orbitals becomes particularly evident when computing the index of the greatest breadth of the brain case and the external bi-orbital breadth. It amounts to 91.5 in the pigmy but to 104.1 in the normal type. This implies that in the normal the breadth of the supra-orbital region is considerably larger than that of the brain case but much smaller than in the dwarf. The other super-structures are completely lacking in the pigmy and there is no sagittal nor a nuchal crest, the occipital torus being restricted to a narrow and somewhat elevated line (Figs. 18 and 20). Of course, it must

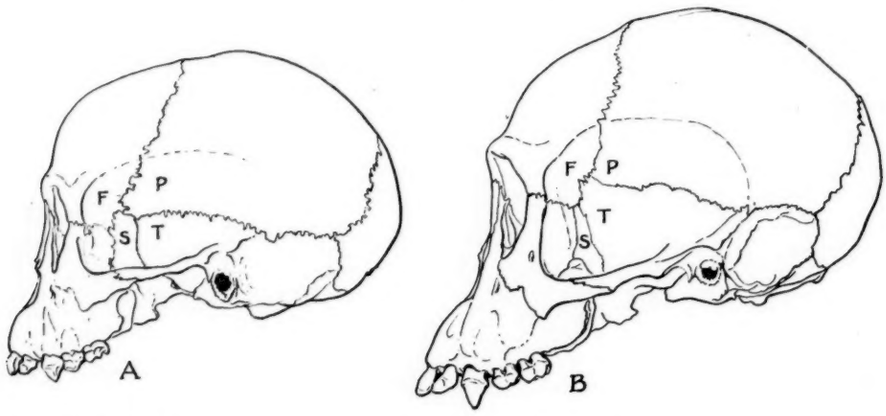

FIG. 21. Skulls of two juvenile types of chimpanzee with complete deciduous dentition (first permanent molar not erupted). Lateral view. 1/2. *A*. Pigmy chimpanzee (*Pan paniscus*), male, Coll. A.M.N.H. no. 86855. *B*. Normal-sized chimpanzee (*Pan schweinfurthi*), male, Coll. A.M.N.H. no. CA 2412. Abbreviations: *F*, frontal; *P*, parietal; *S*, sphenoid; *T*, temporal.

be taken into account that in this case it concerns a female individual in which such features are in no instance as pronounced as in males. The females of the normal type (Figs. 18, 19, 20, *B*), however, reveal that the nuchal crest is strong and well developed in them too. Very characteristic are the differences in the course of the temporal lines. Figs. 18–20 (*lt*) show that they course backwards about half-way along the parietal bone in the dwarf, while they nearly approach the sagittal suture in the normal type. The distance between the lines of either side within the parietal region amounts to 15.5 mm in the normal type but widens to 71.0 mm in the dwarf. Furthermore, that the cranial cavity itself extends much more forward in the latter than in the former can be inferred from the fact that there is no frontal sinus in the pigmy chimpanzee, whereas it is found well developed in the normal type (cf. Coolidge's X-ray photographs of Plate II).

The cranial sutures of the vault are all patent in the pigmy, while fused in the normal type. The figures show that the closure in the special case we selected for comparison because of similar age is already complete but the sutures are not entirely obliterated and

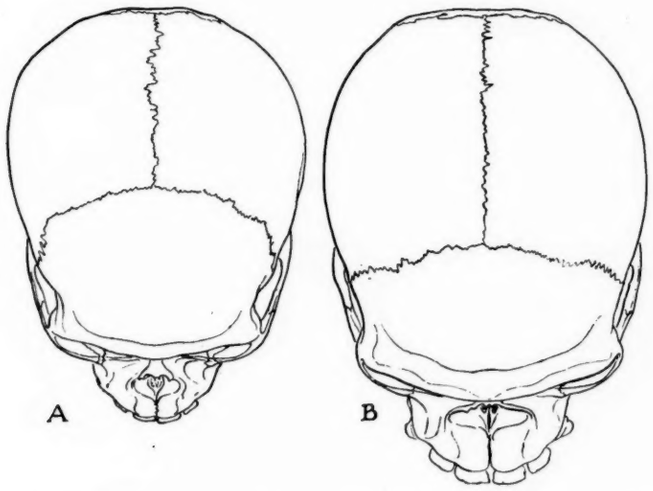

FIG. 22. The same skulls as in Fig. 21 in vertical view. 1/2.

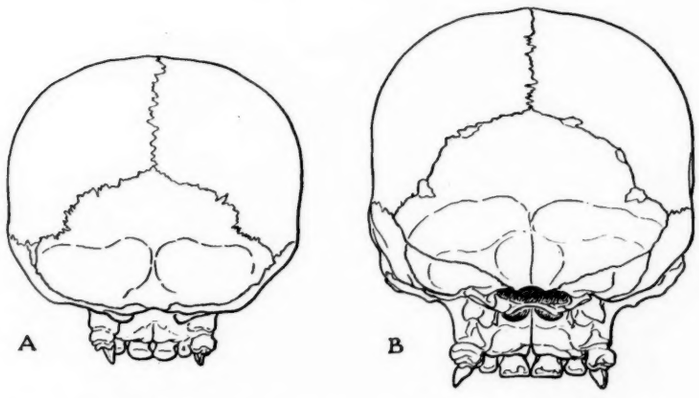

FIG. 23. The same skulls as in Fig. 21 in occipital view. 1/2.

thus still recognizable. Of special interest is the arrangement of the sutures of the pterion region (Fig. 18, *A*) in the pigmy chimpanzee. It is a well known fact that in chimpanzee, as in the two other anthropoids, the frontal and temporal bones come to immediate contact, while in consequence thereof the sphenoidal and parietal bones remain separated from each other (Fig. 18, *B*). In the pigmy chimpanzee, however, the arrangement of the adjacent bones is different. Here, as in man, the sphenoidal and parietal bones are in actual contact and the frontal and temporal bones prevented from adjoining, the length of the line of contact measuring 7.5 mm on the left side. We shall return to this striking phenomenon later.

The upper jaw of the dwarf, as already mentioned above, is smaller in all dimensions, in height, in breadth and in length. The reduction in height may be responsible for the insignificant difference in degree of prognathism between pigmy and normal type, the facial angle being 62° only in the first against 60° in the latter.

The maxilla is shorter and broader in the pigmy and the same is true of the palate and the dental arch as proved by the maxillo-alveolar and length-breadth indices of the palate (cf. Table XVI), but the differences are slight, amounting to only 7 and 4 units, respectively. The teeth are considerably smaller in the pigmy. This applies to all the teeth but in particular to the upper canine (Fig. 18). The diastema only 1.7 mm wide appears rather narrow. The tooth pattern does not differ from that of the normal type. The general character of the mandibles is not distinctly differentiated but it may be of significance that the tori transversi inferior and superior and the fossa genioglossi are much less developed in the pigmy. The teeth are crowded within the mandible and show certain irregularities in position. The canine is small and there is no diastema. No differences can be noted on the pattern of the teeth.

TABLE XVII

MEASUREMENTS AND INDICES OF THE SKULLS OF A JUVENILE MALE PIGMY CHIMPANZEE AND A JUVENILE NORMAL-SIZED SPECIMEN OF THE SAME AGE AND SEX

A. Measurements (in mm)

	Pan paniscus ♂ (A.M.N.H. no. 86855)	*Pan schweinfurthi* ♂ (A.M.N.H. no. CA 2412)
Total length of the skull (*op-pr*)	123	145
Greatest length of the cranium (*g-op*)	101	113
Endocranial length	97	100
Greatest breadth:		
a. Biauricular	73	88
b. Parietal	84	93
Length of the palate	26	34
Breadth of the palate	39	47
Cranial capacity in cc	260	350
Facial angle	78°	69°
B. Indices		
Endocranial and total length of the skull	78.8	68.8
Length-breadth (*b*) index of the cranium	83.1	82.3
Length-breadth index of the palate	150	138

The male juvenile pigmy chimpanzee (no. 86855) already shows the same characteristic differences from the normal type as the adult stage. For the purpose of comparing this skull with one of the normal type, a juvenile male of approximately the same age (CA, 2412, Coll. A.M.N.H.) was selected in which all the deciduous teeth had erupted but with the first permanent molars still entirely embedded within the jaw. As may be seen from Table XVII and Figs. 21–23 the skull of the pigmy is considerably smaller than the type. Notwithstanding the fact that all juvenile chimpanzees of such an age have brain cases more vaulted and globular and proportionally much larger than the face, these peculiarities are much more apparent in the juvenile pigmy than in the type form. The cranial capacity of the pigmy amounts to only 260 cc against 350 cc in the type specimen, but the ratio between the length of the cranial cavity and the total length of the skull is 78.8 in the former against 68.8 in the latter. The forehead of the pigmy is erect and

vaulted with the supra-orbitals only faintly indicated and the parietal tubera already distinct. In the type the forehead recedes, the supra-orbitals are heavier and the parietal bones flatter. Super-structures, of course, are lacking in both cases and the sutures are open. The surprising fact, however, is that in the juvenile pigmy also the arrangement of the pterion sutures is exactly the same as in the adult, showing the typical "human" pattern, namely the sphenoidal and parietal bones in broad contact and the frontal and temporal bones correspondingly separated (Fig. 21, *A*). The type (Fig. 21, *B*) displays the conditions characteristic of the chimpanzee. Furthermore, it should be noted that in the juvenile pigmy the foramen magnum already occupies a more central position than in the type (Fig. 23, *A* and *B*) and that the parietal bone reaches a thickness of only 2.5 mm against 4.5 mm in the type.

TABLE XVIII

MEASUREMENTS OF THE DECIDUOUS TEETH OF A MALE JUVENILE PIGMY CHIMPANZEE (*Pan paniscus*) AND A JUVENILE NORMAL-SIZED SPECIMEN OF THE SAME SEX

	Pan paniscus ♂ (A.M.N.H. no. 86855)		*Pan schweinfurthi* ♂ (A.M.N.H. no. C.A. 2412)	
i^1				
Length	7.6	38	10.0	65
Breadth	5.0		6.5	
i^2				
Length	5.7	26	7.4	41
Breadth	4.5		5.6	
c^1				
Length	7.1	35	8.9	52
Breadth	5.0		5.8	
m^1				
Length	6.6	43	7.7	62
Breadth	6.5		8.0	
m^2				
Length	7.1	59	9.8	97
Breadth	8.3		9.9	

As to the face, the upper jaw is relatively distinctly smaller and less prognathous in the pigmy (Fig. 21), the facial angle being 78° compared to 69° in the type. The palate and the dental arch are clearly broader in the pigmy, the length-breadth index of the former amounting to 150 against 138 in the type.

In regard to the deciduous teeth, it is noteworthy that not only the size is strikingly inferior to that of the type but also that the first molars have a much weaker developed cingulum. In addition, the cusps are more pointed and the wrinkles and crests not as marked as in the normal type. The exact differences in size can be gathered from Table XVIII. It follows from these figures that each type of the deciduous teeth of the pigmy is smaller by about one-third than that of the normal type, while the skull as a whole differs only by one-fourth to one-fifth.

The skull of "Prince Chim" (no. 54336, Coll. A.M.N.H.) belongs to a juvenile male individual. Since his first permanent molars are fully erupted, he must be considered

one or two years older than the pigmy no. 86855. The skull, indeed, is correspondingly larger than the latter, its total length being 141 mm and its cranial capacity (according to Coolidge) 288 cc. The skull of a normal juvenile *Pan schweinfurthi* of the same sex and dentition selected for comparison had a total length of 144 mm. When compared with this skull "Prince Chim" failed to show any really essential differences. It is somewhat smaller but not so much as to justify its being directly ranged within the pigmy group. In conformity to the size of the skull, all the features characterizing the pigmy are lacking in this case. Also the sutures of the pterion region show the arrangement common for the chimpanzee type. However, it is curious that a distinct metopic suture persists, as already stated by Coolidge. This, as far as I know, is the only instance of such a suture ever having been observed in a chimpanzee.

I did not have the opportunity of studying the three additional skulls of the pigmy chimpanzee collected subsequently and awaiting description by Dr. Harold J. Coolidge. He very kindly supplied me with the information that they conform in their general appearance to skull no. 86857. As to details, according to Coolidge, a genuine diastema does not occur in these cases but, on the other hand, two of the skulls show the same "human" arrangement of the pterion sutures described above for the adult and juvenile dwarfs.

Other cases of dwarfism among anthropoids are not known but one of gigantism in which the cranial characters deviate in opposite direction was observed by Hill (1939) in an orang-utang. The orang-utang described by Hill represents a male Sumatran specimen. The total stature amounted to 1581 mm and the total arm-stretch to 2541 mm. Unfortunately, the body-weight is not given. The maximum length of the skull, including the incisors, totals 265 mm but the endocranial length only 112 mm, the cranial capacity being 400 cc. The height of the face amounted to 135 mm. Hill supplies for comparison some corresponding measurements for an adult male Bornean orang-utang which he considers a normal-sized individual. In completing these data by the addition of those available from other sources, it is possible to define the difference in the relation between the total length of the skull and the endocranial length, and facial height and endocranial length in the giant and normal-sized types. The first ratio amounts to 42.3 in the former and to 51.0 in the latter, the second to 120.5 and 98.2, respectively. According to Hill, the preserved brain weighed 335 g. Thus, I do not believe I commit an error if I estimate the body-weight of the giant to be 90 k, and the ratio of brain-weight to body-weight at 1 : 270. Following Dubois (1914), the average of the brain-weight of orang-utang should be 400 g, of the body-weight 73.5 k and the ratio 1 : 184. Dubois' figures are certainly too high as average values.

The photograph of the skull produced by Hill (1939, Pl. 1) shows, in accordance with these figures, the enormous size of the face when compared with the cranium, and this disproportion appears still more pronounced when held against a normal-sized skull. The degree of prognathism corresponds to the difference in size of the jaws. The facial angle amounts to 30° in the giant against 35° in the normal type, according to Hill. Also with respect to other peculiarities the Sumatran orang fits rather well into the plan of giant types. Hill compares it with man and states: "Of the head, the great development of the masticatory apparatus, contrasted with the small size of the neurocranium and sensory components is remarkable, and in direct contrast to the human condition. . . . Many details of skull structure are in noteworthy contrast to the human counterparts, such as the early closure of the cranial sutures, the arrangements of the pterion. . . ."

Whether this Sumatran orang is the representative of a special local giant race or only an individual variation does not matter. Gigantism, in any case, affects form and proportions of the skull in the same way.

It may be justified to include here one other case of dwarfism within the primate group, namely *Symphalangus Klossi* which has been classified as a pigmy form of *Symphalangus syndactylus*. *Symphalangus Klossi* is considerably smaller than *Symphalangus syndactylus* but has some special features in common with the latter as, for instance, the color of the pelage and the syndactylism of the second and third toes. But in regard to the skull, the differences between both types in body size, the relation between the roominess of the cranial cavity and the size of the skull, and the reduction of the face are not greater than those between *Symphalangus syndactylus* and other species of Hylobatids. If the ratio between brain-weight or cranial capacity and body-weight is taken as a basic criterion for determining the dwarf character of a given type, then *Symphalangus Klossi* can no more be considered a dwarf form of *Symphalangus syndactylus* than any of the gibbons. On the contrary, this ratio, according to Schultz (1933) in *Hylobates* even amounts to 1 : 50 (brain-weight 88 g, body-weight 4485 g), while it is only 1 : 73 in *Symphalangus Klossi* (brain-weight 79 g, body-weight 5800 g) against 1 : 96 in *Symphalangus syndactylus* (brain-weight 111 g, body-weight 10,700 g). Schultz, in an exhaustive study on the characteristics of *Symphalangus Klossi*, arrived at the conclusion that this type stands rather close to *Hylobates* and thus cannot be counted as a dwarf form of *Symphalangus*. He thus suggested a special genus for it, known as the *Brachytanytes*. Viewed from our standpoint, the various species of Hylobatids, including *Symphalangus Klossi*, all represent to a certain extent pigmy forms when compared with *Symphalangus syndactylus*.

III. The Phylogenetic Transformation of the Human Skull

It has been shown in the preceding pages that the size of the brain or better of the cranial cavity is of decisive influence upon the configuration of the skull: the greater the space required by the brain, the more other parts of the skull must suffer and necessarily yield to that need. This holds good, in particular, for the face and its essential constituents the jaws. The change the cranium itself undergoes implies the assumption of a more globular shape; the cranium as a whole becomes shorter, broader and higher. The forehead is erect and vaulted, the frontal bone fully participating in the direct formation of the anterior wall of the brain case; the occiput is globular, the greatest breadth being shifted from the base upward to the parietal bones with the development of typical parietal tubera. The walls of the cranium get thinner and the tendency towards an early closure of the sutures is superseded by a trend to remain patent for a much longer period. The face, particularly the upper jaw, becomes reduced in height and length. Instead of continuing the length axis of the cranium in a forward direction, the face seems to have been moved backward so as to underlie the frontal portion of the cranium. Palate and dental arch have become short and broad. The teeth share in the general reduction of the jaw in that the crowns and roots not only become considerably smaller but also show a distinct tendency towards simplifying their pattern by losing to a certain extent such structures as the cingulum, cusps and crests. The reduced size of the masticatory apparatus combined with the relative increase of cranial capacity results in diminution or complete disappearance of the super-structures of the cranium. The supra-orbitals or their corresponding forma-

tion (postorbital process and its root) become thinner and less prominent or disappear entirely. The same is true of the sagittal and nuchal crests and their special differentiations. The temporal lines shift downwards and cross the parietal bone at one half of its height or even lower. The frontal sinuses are lost or considerably diminished in size and extension.

All these modifications and differences distinguishing the skull of a dwarf type from that of a normal large one also constitute the characteristic dissimilarities between the skull of recent man and that of an anthropoid, especially the chimpanzee and gorilla, whereby the anthropoids represent the "normal" or large type and man the dwarf. Such a definition may perhaps at first glance seem unreasonable, for it is evident that man cannot be considered a dwarf if the giant form is represented only by a mere chimpanzee or gorilla. It must be borne in mind, however, that the essential factor upon which our comparison is based concerns only the size of the brain and the brain case, respectively, in relation to the remaining part of the skull. In the case of the dwarf dogs or the pigmy chimpanzee, the relative size of the brain was exchanged for a general decrease of the size of the body. In man, however, such did not take place, the brain having increased without impairing the body parts. The effect upon the formation of the skull must, of course, be the same regardless of whether that increase is relative or absolute, for the increase alone serves as the decisive factor for the configuration of the definitive form. We will revert to this question later on.

In dog and chimpanzee dwarf and large types constitute variations of one and the same species. But it has been shown above that within the group of platyrrhine monkeys quite differing genera, like the marmoset, also correspond in regard to the skull form to the dwarf type but others, like the howler, to the large ones. Taxonomically, man must be classified among the anthropoids. He can, therefore, be compared with the gorilla or chimpanzee with as much justification as the marmoset with the howler. In the platyrrhine case, however, we have no knowledge of the phylogenetic relationship but it may be supposed that both types originated from a common stock which underwent certain diverging differentiations in the course of evolution, one of which is represented by the marmoset and the other by the howler. In man the condition is quite different. We know that the form of recent man must be regarded as the result of a continuous transformation of an anthropoid fairly close to the present day gorilla or chimpanzee. Palaeontology provides us with some of the intermediate stages linking the supposed but still unknown original form and the final product. The most primitive and thus closest to the anthropoids are the prehominids: *Pithecanthropus* and *Sinanthropus*, followed by the various types ranged under the collective name "Neanderthal Man" but representing at least three different evolutionary and subsequent stages. Since this is not the place to enter into a discussion of the morphological facts supporting the sequence applied to the fossil forms, the reader is referred to my recent publications on this subject (1939 b—Lectures I and V, 1940 c), to those of von Koenigswald (1937, 1938, 1939) and to the joint article of von Koenigswald and myself (1939). For the correct understanding of the evolutionary process it is important not to underestimate the fact that all of the human fossils known thus far display an extensive transformation of the skull, whereas the remaining skeletal parts are much less affected, apparently because they had become adapted to the erect posture at a much earlier stage and, therefore, show a closer resemblance to the correspond-

ing bones of recent man. When an anthropoid skull of the general appearance of gorilla, that is to say, a large type, as far as the correlation between brain case and skull as a whole is concerned, serves as an example of the original form of human evolution, the intermediate forms show in principle all the characteristic changes of the skull which—*mutatis mutandis*—are exhibited in the dog series leading from the Irish wolfhound to the King Charles spaniel.

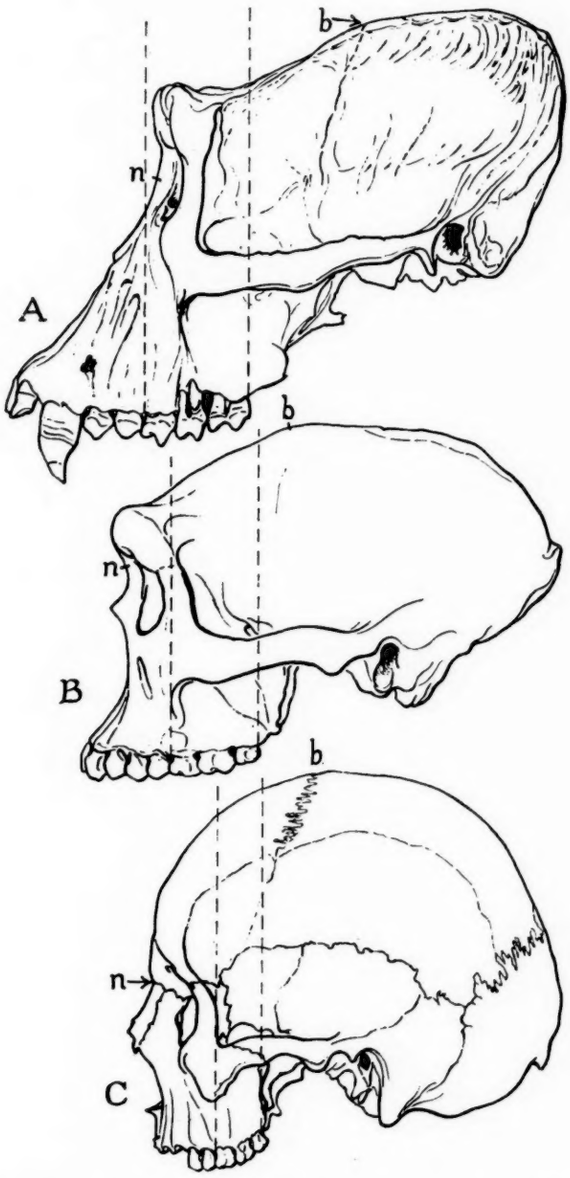

FIG. 24. Skulls of gorilla, *Pithecanthropus* and modern man. Lateral view. 1/3. *A*. Adult male gorilla, Coll. A.M.N.H. no. CA 506. *B*. Reconstruction of the male *Pithecanthropus* skull IV (cf. von Koenigswald, 1939, and Weidenreich, 1940). *C*. Modern man (European), male, Coll. A.M.N.H. no. 3818.

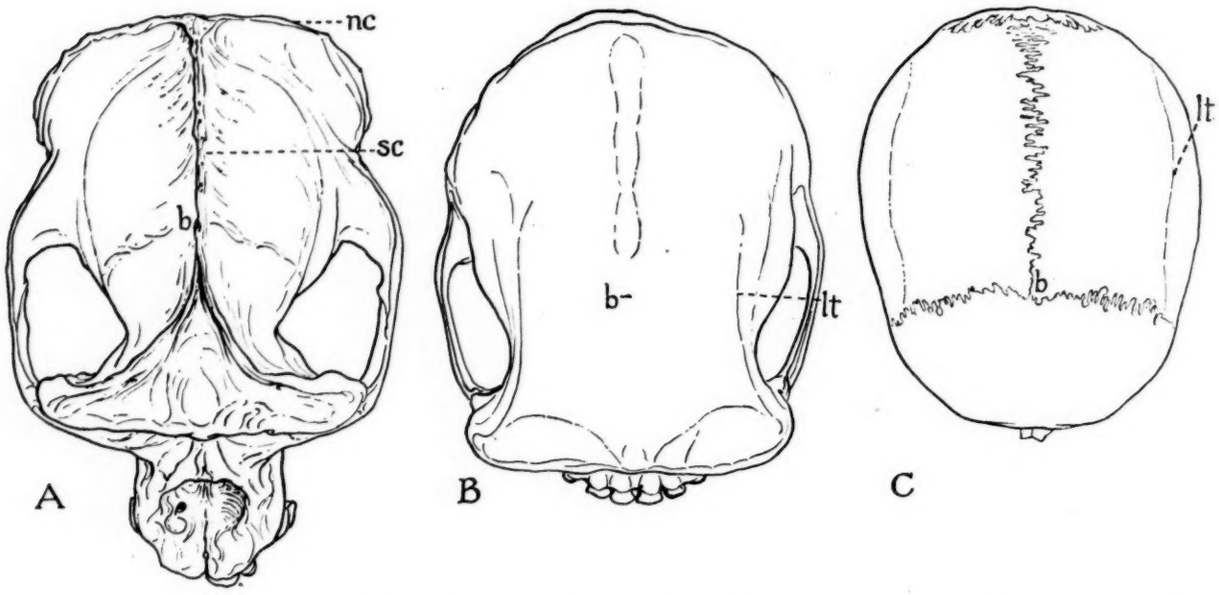

FIG. 25. The same skulls as in Fig. 24 in vertical view. 1/3. Abbreviations: *lt*, temporal line; *nc*, nuchal crest; *sc*, sagittal crest.

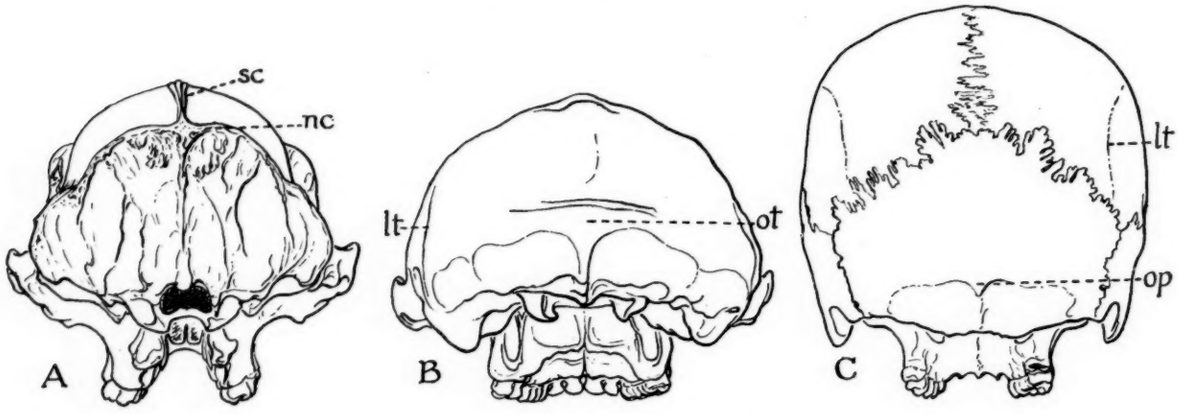

FIG. 26. The same skulls as in Fig. 24 in occipital view, except that skull *A* represents an adult female gorilla, Coll. A.M.N.H. no. 54356. 1/3. Abbreviations: *lt*, temporal line; *nc*, nuchal crest; *ot*, occipital torus; *op*, occipital protuberance; *sc*, sagittal crest.

In order to illustrate the morphological differences of the skulls of the supposed anthropoid-like ancestor, the most primitive intermediate stage and recent man, I placed side-by-side in Figs. 24–26 the skulls of an adult male gorilla (Coll. A.M.N.H. no. CA 506), the reconstruction of the adult male *Pithecanthropus* Skull IV and the skull of a modern European of unknown origin (Coll. A.M.N.H. no. 3818). The reconstruction of the adult male *Pithecanthropus* Skull IV is based on the cranial fragments and the pertaining upper jaw recovered by R. von Koenigswald in 1939, briefly mentioned by him in the Year Book of the Carnegie Institution (1939) and described in a joint publication, von Koenigswald

and Weidenreich, 1939. Under the title "Man or Ape," in an article published in Natural History (1940) I described the method of reconstruction of this skull executed at the Palaeontological Laboratory of the American Museum of Natural History in New York. Since no other facial part but the upper jaw is preserved with the frontal cranial bones also missing, the reconstruction of the superior portion of the face, including the forehead, is more or less arbitrary. But as the forehead and the supra-orbitals are partly preserved in Dubois' *Pithecanthropus* Skull I and von Koenigswald's Skull II (1938), we have a fairly accurate basis on which to restore the missing parts of Skull IV. It must be taken into account, however, that Skulls I and II apparently belong to female individuals, while Skull IV is that of a male. The supra-orbitals of Skull IV must, therefore, have been broader, higher and more salient and its forehead flatter than in Skulls I and II. Since the preserved parts of Skull IV comprise two-thirds of the brain case, namely the entire posterior region up to bregma, the basal portion up to the pterygoid fossae and the upper jaw, the height and breadth of the cranium are given. The glabella-opisthocranion length can easily be computed from the length of the upper jaw as well as from the length of the preserved base. Thus, only the face and the forehead of the reconstruction may be incorrect in details but the general form cannot be too far removed from the original condition and, in any case, is sufficiently reliable to represent an intermediate hominid type for a comparison with the anthropoid-like starting form on one hand, and the terminal phase, recent man, on the other.

The lateral view of the three skulls (Fig. 24) shows the characteristic differences in the configuration of the entire skulls and in the relation between size and form of the brain case and face. In gorilla (*A*) the brain case is long and low, while it is relatively short and high in recent man (*C*), that is to say, there is a distinct tendency in the latter towards assuming a globular form. In correspondence therewith, the great ape lacks a forehead, the frontal bone being in recumbent position, while the occiput appears elongated in the upward and backward directions. In man the forehead is erect and well vaulted, the occiput rounded and extending downwards considerably.

The face of the gorilla is characterized by heavy and far-protruding supra-orbitals which are separated from the brain case by a wide furrow-like depression and thereby represent a real superior boundary of the face. The upper jaw is high and long, projecting considerably beyond the termination of the nasal bones. In man the supra-orbitals have disappeared completely, the frontal bone taking part in shaping the superior portion of the face. The upper jaw is reduced in height and length and, in the special case illustrated in Fig. 24, the anterior surface of the alveolar process is retracted as far behind as the frontal plane of the nasal bridge.

The super-structures of the cranium are strongly developed in gorilla. In addition to the heavy supra-orbitals just mentioned, there is a high sagittal crest which starts before the bregma at the junction of the temporal lines, merging within the lambda region into a high and broad nuchal crest and then extends forwards and downwards toward the mastoid region of the temporal bone (Fig. 25, *A*). In man the supra-orbitals and sagittal crest have become lost completely, the nuchal crest being reduced to an insignificant occipital protuberance and the mastoid process entirely isolated, so that it now seems to represent quite an independent formation. The temporal line is fine and not elevated and at no point reaches the midline of the cranium, coursing approximately half-way between this

line and the squamosal suture. The cranial sutures are almost entirely obliterated in the gorilla, while still rather distinct and partly open in the illustrated case of man.

The vertical views of the skulls (Fig. 25) complete this picture. They show in particular the ovoid form of the brain case proper in gorilla (*A*) and the more globular one in man (*C*), the extraordinary development of the super-structures in the former and their complete absence in the latter, and finally the extreme prognathism of the upper jaw of the ape and its complete retraction in man. As a consequence of the relative smallness of the brain case and the excessive development of the jaw and the super-structures, in

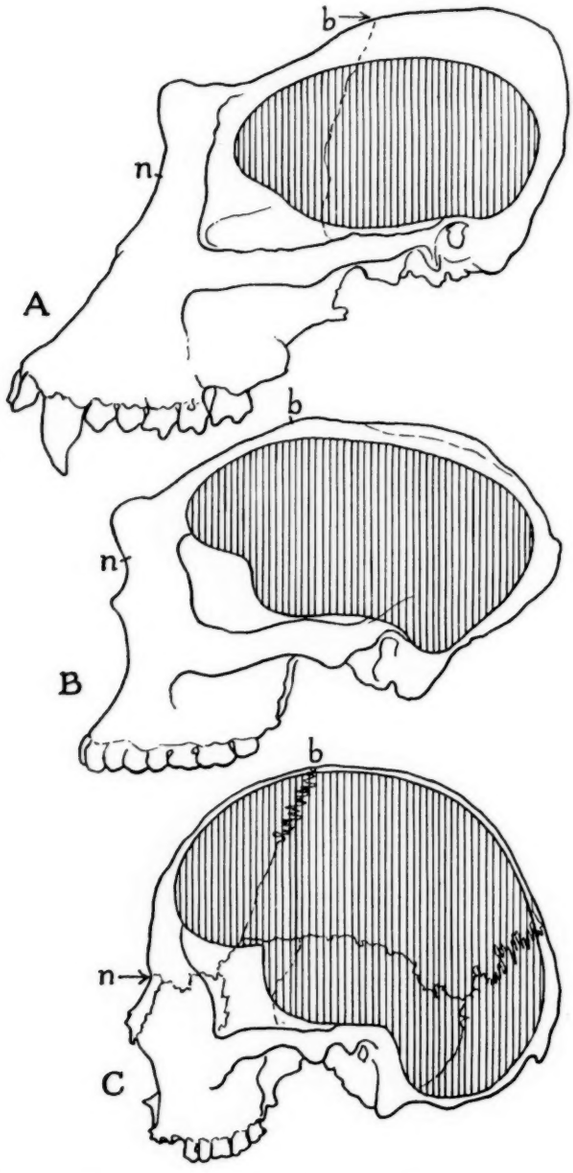

FIG. 27. The same skulls as in Fig. 24 with comparative dimensions of cranial cavities (shaded). 1/3.

particular of the supra-orbitals, there is a deep postorbital constriction in gorilla combined with a considerably projecting zygomatic arch, while the constriction is entirely missing in man and the compact zygomatic arch is so close to the lateral surface of the brain case as to be completely concealed under the parietal bulge of the cranium.

The extension of this parietal bulge is especially marked if the skulls are viewed from behind (Fig. 26). The brain case of the gorilla (*A*) appears low as a whole and strikingly broad at the base with the lateral walls gradually receding toward the crown. In man the brain case is extremely high and its base relatively narrow while the greatest breadth has shifted upwards toward the parietal bone (*C*). The occipital view demonstrates also very impressively the differences in the character and orientation of the temporal line which in the ape forms the sagittal crest (*A*, *sc*) while in man it retains its linear structure and crosses the parietal bone at the level of the tuber region. The differences in localization of the foramen magnum are likewise evident. In gorilla the foramen is situated near the posterior pole of the occiput with its opening chiefly directed posteriorly (*A*); in man it occupies almost the center of the base and is usually directed anteriorly so as to become invisible when viewed from behind (*C*).

Pithecanthropus Skull IV follows in all of the features described above the middle course, bearing a closer resemblance to anthropoids in certain respects and to recent man in others. Of similarity to the gorilla are the length and lowness of the brain case, especially the flatness of the forehead and its greatest breadth coinciding with the biauricular breadth (Fig. 26, *B*) and, moreover, the breadth and bulkiness of the supra-orbitals (Figs. 24 and 25, *B*) and the orientation of the mastoid process (Figs. 24 and 26, *B*) which appears as a thick protuberance superposed on the lateral surface of the mastoid portion as a continuation of the occipital torus rather than as an isolated process in downward direction (Fig. 26, *B*). On the other hand, super-structures such as the sagittal and nuchal crests are missing. The temporal line runs backwards at some distance from the median line (Fig. 25, *B*), the site of the sagittal crest itself being occupied by a curious high and broad longitudinal tuber mainly restricted to the vertex (Figs. 24 and 26, *B*). There are no indications anywhere of its joining either the temporal line or the similarly heavy tuber structure in the inion region. The latter (Figs. 24–26, *B*) corresponds to the occipital tuber, a rather common feature in fossil skulls of man, which in the case of *Pithecanthropus*, however, has attained extraordinary dimensions. As to the face, the upper jaw when compared with that of recent man (Fig. 24, *B* and *C*) is rather long and broad and extremely prognathous, with scarcely an indication of a nasal spine. Moreover, it should be noted that the superior end of the pterygoid process is occupied by a large sinus, a regular occurrence in the gorilla but very rare in recent man and, if at all present, never of such extent.

Of special interest is the size of the cranial cavity in proportion to the skull in the three types compared: gorilla, *Pithecanthropus* and recent man. Figs. 27 and 28 illustrate an attempt of outlining the extension and localization of the cranial cavity within the skull in both lateral and vertical views. The difference between gorilla (*A*) and man (*C*) is striking. One must, of course, bear in mind that the capacity of the gorilla skull amounts to only 445 cc against 1430 cc in the human skull and that the enormousness of the cranium of the adult male gorilla is merely brought about by the super-structures and not due to the size of the brain case itself, for the walls proper of the simian brain case are not stronger than those of man if the super-structures are disregarded. In comparing the drawings

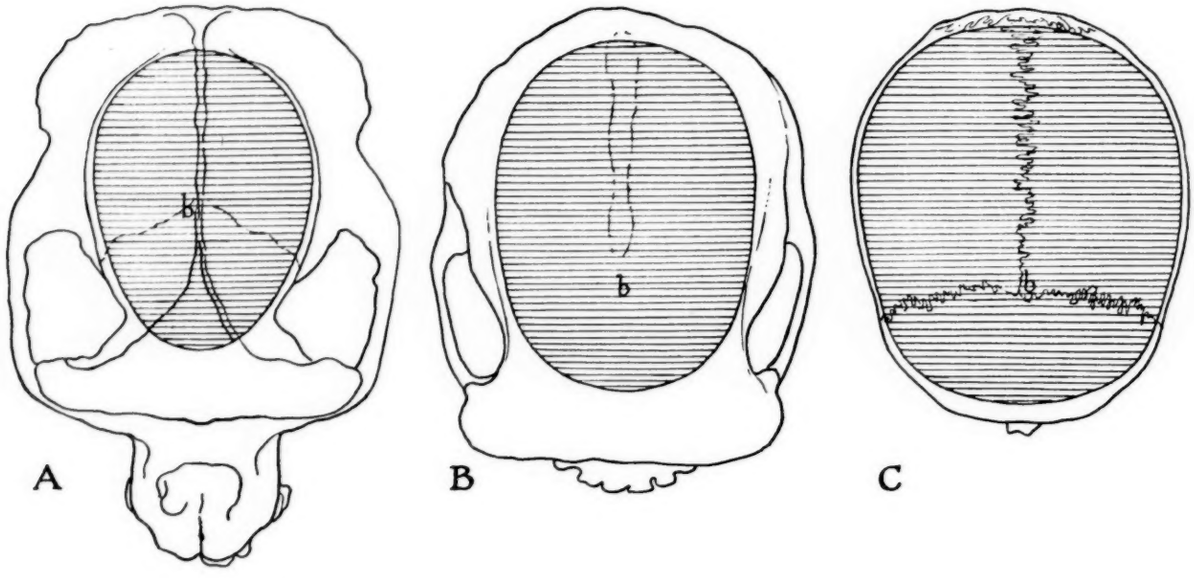

FIG. 28. The same skulls as in Fig. 25 with comparative dimensions of cranial cavities (shaded). 1/3.

with those of the dwarf and large dogs (cf. Figs. 27, 28 and 4, 5), the similarity is striking, the only difference being that in gorilla the anterior pole of the cranial cavity extends considerably further beyond the coronal suture, while in the Irish wolfhound it scarcely surpasses this line. But as in the latter case, there remains a considerable space between the anterior end of the cavity and the outer contour of the face, the space being occupied by a large frontal sinus. Fig. 29 shows the skulls of an adult male gorilla and recent man reduced to the same dimensions in cranial cavities. The region above the nasion and

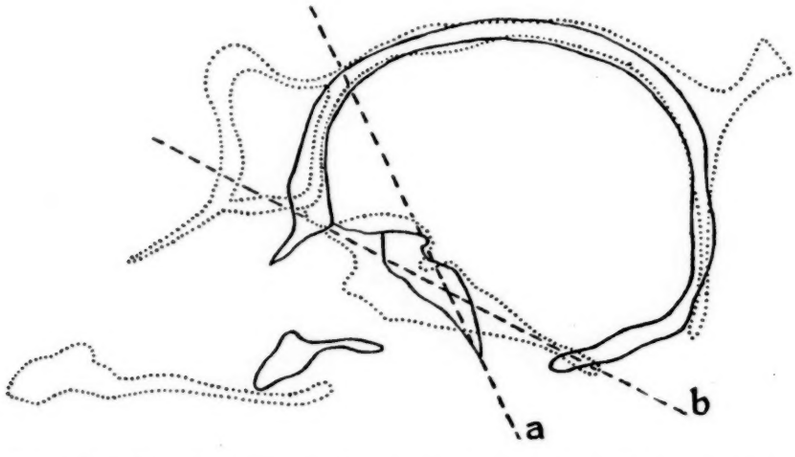

FIG. 29. Diagrams of median sections through the skulls of gorilla (dotted line ····) and man (continuous line ——), the two skulls being reduced to the same endocranial size and superposed in the porion-suborbital horizontal.

occupied by the supra-orbitals in the case of the ape contains a large sinus with two separate walls, the posterior one of which comprises the anterior wall of the brain case, and the anterior one the facial surface. In man there is only one wall which is split into two lamellae with the frontal sinus restricted to a relatively narrow cleft between them (not indicated on Fig. 29). The cranial cavity of *Pithecanthropus* Skull IV (c. 900 cc) is approximately twice the size of that of the gorilla (Figs. 27 and 28, *A*, *B*) but considerably smaller than the average of recent man. The walls in this case, however, as well as in the other *Pithecanthropus* skulls are of an extreme thickness, far in excess of the conditions found in man and anthropoids (cf. Chapter I). This particularly is specific to fossil man, especially to prehominids, but pending further material cannot be explained satisfactorily.

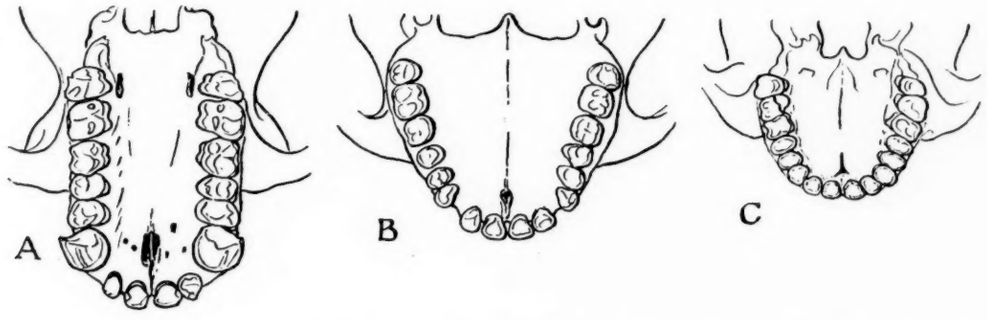

FIG. 30. Palate and dental arches of an adult male gorilla, *Pithecanthropus* Skull IV and modern man. 1/3. *A*. Gorilla, Coll. A.M.N.H. no. CA 505. *B*. *Pithecanthropus*. *C*. "Old Man" of the Upper Cave of Choukoutien, PA No. 101.

Palate and dental arch participate in characteristic manner in the reduction of the upper jaw and the alteration of its form depends thereon. As is evident from Fig. 30, palate and dental arch of the gorilla (*A*) are long and narrow with the premolar-molar rows running almost parallel in straight lines, whereas in man (*C*) palate and dental arch form a short and wide parabolic figure with the premolar-molar rows diverging. *Pithecanthropus* Skull IV (*B*) is also in this respect intermediate between anthropoid and man. A comparison of the corresponding behavior of palate and dental arch in dogs (cf. Figs. 6 and 30) again shows an astonishing parallelism between dwarf type and man, and large type and gorilla.

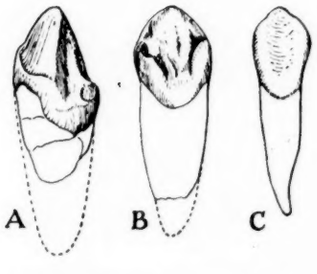

FIG. 31. Canines of the anthropoid-human line. Lingual side. 1/1. *A*. C_1 *rt* of a fossil orang-utang. *B*. C^1 *rt* of *Sinanthropus pekinensis*. *C*. C_1 *rt* of modern man.

The dentition reveals the same principle. The human teeth (Figs. 31–33) are not merely smaller than in gorilla but also show an identical tendency of simplifying their pattern. The cingulum so characteristic a feature of the anthropoid tooth becomes completely lost in man (*C*); the cusps not only undergo a diminution in size but also in number and the crests and wrinkles have become replaced by an almost entirely smooth surface. In this regard also *Pithecanthropus* occupies an intermediate position between anthropoids and recent man; *Sinanthropus*, whose dentition served as example illustrated in Figs. 31–33, resembles in some characteristic variations the anthropoid form more than he does recent man. In dwarf and large dogs, however, the fundamental nature of the dentition does not change; it is and remains a canine dentition. The same, of course, holds good for the anthropoid-human line; the basic character as an anthropoid dentition is unaltered throughout all the stages as is particularly evident in the retention of the *Dryopithecus* pattern by the lower molars.

FIG. 32. Second lower premolars of the anthropoid-human line. Occlusal view. 1/1. *A*. P_2 *rt* of chimpanzee. *B*. P_2 *rt* of *Sinanthropus pekinensis*. *C*. P_2 *rt* of modern man.

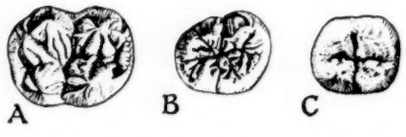

FIG. 33. Lower molars of the anthropoid-human line. 1/1. *A*. M_1 *lt* of gorilla. *B*. M_2 *lt* of *Sinanthropus pekinensis*. *C*. M_2 *lt* of modern man.

One other parallelism between the canine and human line concerns the position of the upper molars in relation to the expansion of the cranium (Fig. 4). In the case of the gorilla (*A*) the vertical interrupted lines which delineate the molar row (Fig. 24) fall entirely before the anterior pole of the brain case and within the zone of the supra-orbital region. In man (*C*), however, they run through considerably behind the corresponding region indicating that the molar row completely underlies the frontal section of the cranial cavity. *Pithecanthropus* (*B*) is in this respect again between gorilla and man.

To express the differences of the forms discussed with the aid of the usual measurements and figures meets with certain difficulties. In the case of the dog, the brain case is located behind the face in such way that the longitudinal axes of the two components of the skull form an almost continuous straight line; the total basal length of the skull, that is to say, the distance from the basion to the prosthion therefore corresponds to the real extension of the cranium plus face. In primates, especially in the higher groups, however, the topographical relation between brain case and facial bones undergoes a rather significant change. The brain case shows the increasing tendency to overlap the facial bones with the final effect that in recent man the latter come to lie under the anterior portion of the brain case. Fig. 34 (taken over from Duckworth, 1915) where the median sections of the skulls of dog (*A*), male gorilla (*B*) and recent man (*C*) are placed side-by-side shows this change

rather impressively. But it should be noted that the dog skull (*A*) illustrated by Duckworth apparently represents the skull of a large type, for in dwarf dogs like the King Charles spaniel given in Figs. 1–3 (*A*) the translocation described above is almost identical to that occurring in man, in both cases in consequence of the enormous expansion of the brain case at the expense of the facial parts. On account of these altered positions the basal length (basion-prosthion) of the anthropoid or human skull is in no way equivalent to the same measurement on the skull of a large dog. As is evident from Fig. 34, *B* and *C*, it does not even cover comparable distances in gorilla and man. So as to obtain better comparable results than those just described, I made use in the case of the higher primates

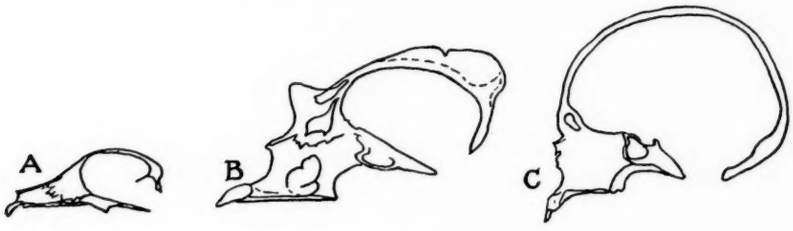

FIG. 34. Median sections through the skulls of a dog (*A*), a male gorilla (*B*) and a male native of New Britain (*C*), after W. L. H. Duckworth (1915).

of the distance from the opisthocranion to the prosthion, though fully aware that this measurement is also inadequate.

Table XIX contains measurements of the three skulls of the anthropoid-human line which correspond to those of the dog skulls in Table VI. The figures show that in recent man the length of the cranial cavity amounts to 89.2 per cent of the length of the whole skull but only to 46.2 per cent in gorilla. This is almost precisely the same ratio as in dogs, with 91.2 per cent for the King Charles spaniel and 45.6 per cent for the Irish wolfhound, *Pithecanthropus* and the bulldog with 70.0 and 63.8 per cent, respectively, ranging in the middle. In respect to the ratio between the length of the face and the length of the cranial cavity, the differences are much greater in dogs with 131 per cent in the wolfhound and

TABLE XIX

MEASUREMENTS (IN MM) AND INDICES OF THE THREE SKULLS OF THE ANTHROPOID—HUMAN LINE

	Adult Male Gorilla CA 505	*Pithecanthropus* Skull IV (rest.)	Recent Man Adult Male No. 3818
Total length (*op-pr*)	250	220	185
Endocranial length	115	155	165
Greatest cranial length (*g-op*)	158	199	176
Facial height (*n-pr*)	131	85	72
Cranial capacity in cc	445	c. 900	1430
Ratio between total and endocranial length	46.0	70.0	89.2
Ratio between facial height and internal length of the brain case	114	54.8	43.7

9.6 in the spaniel, while the corresponding figures for the anthropoid-human line amounts to only 114 and 43.7.[2]

The parallelism between the two extreme types of the canine skull, on one hand, and gorilla and recent man, on the other, even involves the details. But there is one basic difference; the canine types are variations of one and the same species, while gorilla and man, with due allowance, the starting and final phase of a phylogenetic line of evolution. In both cases, however, the volume of the cranial cavity in its relation to the size of the skull as a whole determines the particular shaping of the skull. This relation also governs, as shown above, the configuration of the skull of other orders or groups of mammals and thus appears to be the expression of a biological law of general validity.

IV. The Correlation between the Size of the Brain and Special Shaping of the Skull

The cerebral predominance that characterizes the skulls of dwarf forms and man not only determines the special shape of the brain case proper but also the size and arrangement of the facial parts and, in connection therewith, the development of the super-structures of the cranium. As early as 1857 R. Virchow pointed to the brain case as the decisive factor in the formation of the human skull and especially in the development of the face. He considered in particular the different forms of the cranial base as the main agent responsible for all of the variations in the construction of the face. Ranke (1892) following Virchow's assumption came to the conclusion that there is a close connection between the deflection of the cranial base, the position of the face and the relative size of the brain case. The skull of an ape, according to Ranke, is mechanically workable only if the huge face is combined with a small brain case and brain. On the other hand, a human skull should only be realizable if a large brain case and brain are linked to a small face. According to Ranke, it is the special relation between brain and skull which determines the human type. As long as the volume of the brain case exceeds that of the facial parts, the form of the skull is human; the larger the jaws and the poorer the development of the brain, the greater the deviation from the human type towards the apes.

The deflection of the base of the human skull to which Virchow and Ranke refer, indeed, is characteristic of man. As may be seen from Duckworth's figures (Figs. 29 and 34, *C*) the vertex of the basal angle coincides with the junction of the pre- and postsphenoid. In the gorilla (*B*) there is no deflection, the basal line being almost entirely straight as in dog (*A*).

In an early publication (1924 b) I was able to show that the deflection of the base had to be regarded as a consequence of the adaptation to the erect posture and the enormous expansion of brain and brain case. The upright position would necessitate the skull to adopt extreme flexion in order to bring the face from its primary orientation to the newly acquired plane of vision. Such could not have been attained by flexion in the occipital joint alone but must be supported by an inclination of the base itself. I shall have to revert to this problem later.

The interrupted lines in Fig. 29 demonstrate the degree in which the direction of the base of the human cranium (*a*) deviates from that of the gorilla (*b*). The deflection of the

[2] These figures refer to only individual cases selected for comparison. Nevertheless, they could not differ essentially if the average of a larger number of measurements was taken as a basis.

base, of course, is of some influence upon the general position of the face but it is not responsible for the degree of prognathism, as Ranke believed, and still less for the reduction of the face. This may be inferred from the fact that the cranial cavity and the face of dwarf dogs rival in roominess and smallness, respectively, those of man without the base having undergone the slightest deflection. The correlation between brain, cranial cavity and face, particularly the jaws, is quite independent from the form of the base and merely conditioned by the relative size of the two constituents of the skull. That such a correlation really exists has been acknowledged by all earlier students of this problem from Cuvier to Topinard. In a private discussion with one of the best known anthropologists which followed the delivery of my address on this subject before a meeting of the American

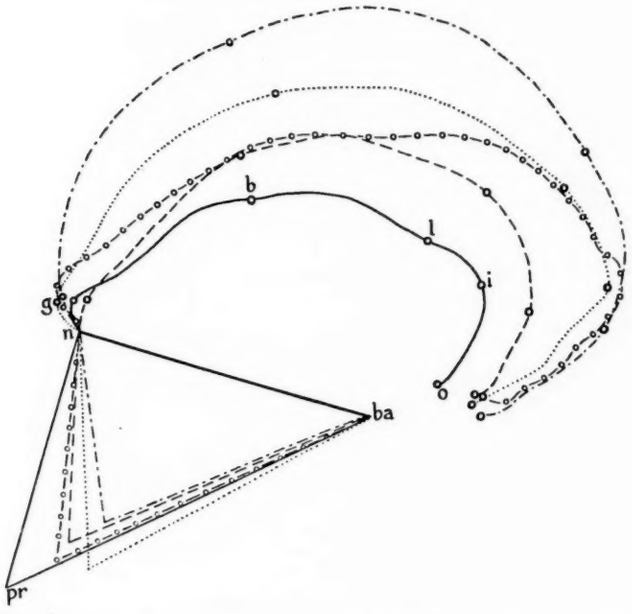

FIG. 35. Diagrams representing median sections of skulls from nasion to opisthion, all reduced to the same nasi-basal length (*n-ba*), combined with the facial triangle (*n-pr-ba*). Chimpanzee ——, microcephalic modern man (Schüttelndreyer) – – –, *Pithecanthropus* Skull IV o–o–o–, Neanderthal Man (Rhodesian) · · · ·, modern man (European) ·–·–·–·

Association of Anthropologists in New York (1940), I was met with the abrupt objection that it was not admissible to speak of correlations between brain case and face since both parts should represent absolutely independent formations. The data already supplied herein, however, prove convincingly, I believe, the correctness of my assumption. In addition, still other facts serve to confirm it.

In the diagram of Fig. 35 the outlines of median sections through the skulls of chimpanzee (——), *Pithecanthropus* Skull IV (o–o–o), a Neanderthal type (Rhodesian Man) (· · · ·) and recent man (–·–·) have been reduced to the same basal length of the skulls (*n-ba*) and superposed on this basal line. The corresponding faces are illustrated by the facial triangle nasion-basion-prosthion (*n-ba-pr*). It is apparent at first glance that the area of the facial triangle is inversely proportional to the size of the brain. It is difficult,

of course, to determine mathematically the correct size or volume of the face for a comparison with the size of the brain case or the cranial capacity. Nevertheless, it is possible to obtain a fairly accurate estimation of these values either by calculating the square millimeters of the surfaces of median sections including that of the lower jaw, as was done by Stratz (1905), or by determining the volume of the face by multiplying the length with breadth and depth. Stratz found that the ratio between cranial cavity and face (including the lower jaw) amounts to 90 in anthropoids but to 42 in recent man (the maximum in man may rise to 50 and the minimum in anthropoids drop to 80). I computed the volume of the face (excluding the lower jaw) by measuring length, breadth, and depth. The height taken is represented by the vertical distance from a plane through the frontal-zygomatic sutures and parallel to the Frankfort plane down to the lowest point of the alveolar process of the upper jaw. The breadth taken coincides with the greatest superior breadth of the face (*fmt-fmt*) and the depth corresponds to the maxillo-alveolar length. Table XXI gives the

TABLE XX

RELATION BETWEEN SIZE OF THE CRANIAL CAVITY AND SIZE OF THE FACE (AFTER C. H. STRATZ, 1905)

Anthropoids	90
Pithecanthropus Skull I (Dubois)	72
Neanderthal man	54
Recent man	42

figures obtained including those of the pigmy chimpanzee, the three dog types, and two human microcephalics to be referred to subsequently. As is evident from the figures, the volume of the face is double that of the brain case in gorilla, of the same size in *Pithecanthropus* but only one-fourth in recent man. In the adult chimpanzee of normal size the face is about three-fourths larger than the brain case, while in the pigmy it is one-eighth smaller. In juvenile individuals where the jaws have not attained their definite size, while the brain case has almost reached its final capacity, the difference between the pigmy and the normal type, of course, is much less but already rather pronounced. In larger dogs the brain case is only one-half or one-third the size of that of the great apes, while the volume of the face is more than six times larger; in dwarf dogs, however, the brain case is about one-third more in volume than the face. In the case of gorilla a female individual was taken for comparison. Since in males the face is much heavier built but the brain case of about the same size, the ratio is considerably greater and not too far removed from that computed for the large dogs. The ratio of 26.3 calculated for recent man, of course, does not include all possible variations, but it may be supposed that it would hardly exceed the 40 mark and not be much below 20.

Although a correlation between the size of the cranial cavity and that of the face cannot be denied, it is not easy to discern which special internal factor should be made responsible. That the deflection of the base cannot be the cause, as was supposed by R. Virchow and Ranke, follows from the simple fact that the correlation is not confined to anthropoids and man but also occurs in carnivores in which there are no indications of a deflection of the cranial base. Correlations of such a nature, however, are rather common in the entire animal kingdom as revealed by recent studies. Julian Huxley assumed them

to be under the category of relative growth (1932). In the special case of skull growth he refers to Zuckerman's statement (1926) that during the later growing period of the juvenile baboon skull the cranium falls more and more behind, while the face shoots forth constantly. Huxley calls such a phenomenon heterogony or allometry (Huxley and Teissier, 1936). In the stage of development referred to, the growth of the baboon brain compared with that of the jaws is negatively allometric. The same holds good for the brain and jaws of anthropoids and large dogs. But in dwarf dogs the conditions apparently are reversed in that the brain leads in relative growth, in other words a positive allometry exists. Man follows the same rule as dwarf dogs, that is to say, the growth of the brain in relation to

TABLE XXI

RATIO BETWEEN VOLUME OF THE FACE AND CRANIAL CAPACITY

	Cranial Capacity in cc	Volume of the Face in cc	Index
Gorilla ♀			
A.M.N.H. no. 54356	405	837	207
Pithecanthropus			
Skull IV ♂	900	905	100
Recent man ♂			
A.M.N.H. no. 3818	1430	377	26.3
Microcephalic Basuto woman	340	236	69.4
Microcephalic Parisian woman	280	180	64.2
Adult chimpanzee (*Pan schweinfurthi*) ♀			
A.M.N.H. no. 90191	350	589	169
Adult pigmy chimpanzee ♀			
(*Pan paniscus*) A.M.N.H. no. 86857	272	240	88.2
Juvenile chimpanzee ♂			
(*Pan schweinfurthi*) A.M.N.H. no. CA 2412	355	198	55.8
Juvenile pigmy chimpanzee ♂			
(*Pan paniscus*) A.M.N.H. no. 86855	255	104	40.7
Irish wolfhound ♂			
A.M.N.H. no. 80250	145	947	653
English bulldog			
A.M.N.H. no. 69453	80	29.6	257
King Charles spaniel ♀			
A.M.N.H. no. 19182	55	36.8	67

the jaws or face is positive allometric. *Pithecanthropus* seems to keep to the middle line. In the baboon skull underlying the argumentation, we are dealing with the ontogenetic development of one and the same individual. In the case of dwarf dogs the allometry concerns different variations of the same species; in one extreme it is positive and in the other negative. However, in the anthropoid-human line the allometry changes its character during the phylogenetic evolution and thereby determines the final form.

It has been shown above that the dimensions of cranium and face, and of cranium and body are closely correlated. That the latter correlation follows the law of relative growth, too, will be shown in the following chapter. But we must first deal once more with the consequence of the alteration of the cranial form brought about by the expansion of the cranium and the reduction of the face.

In all the dwarf types described above, the brain case displays a distinct tendency to assume a more or less globular form (cf. Figs. 1–5, 11–13, 18–23, 24–28). This may be adequately explained by the fact that the sphere is geometrically the most economic form to accommodate a relatively large organ such as the brain within a small skull. As has been shown by Klatt (1921), the brain of a King Charles spaniel (Fig. 36) is relatively short,

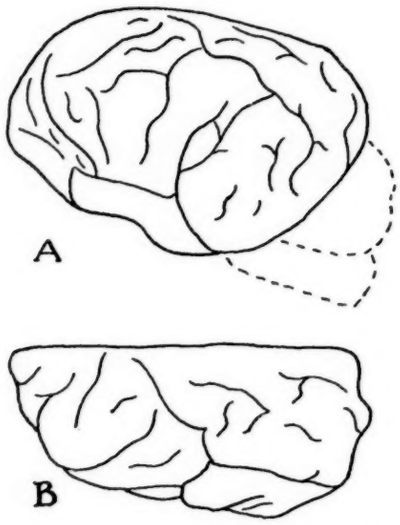

FIG. 36. Brain of a male King Charles spaniel after Klatt (1921). 1/1. *A*. Left side. *B*. Left hemisphere of the same brain from above.

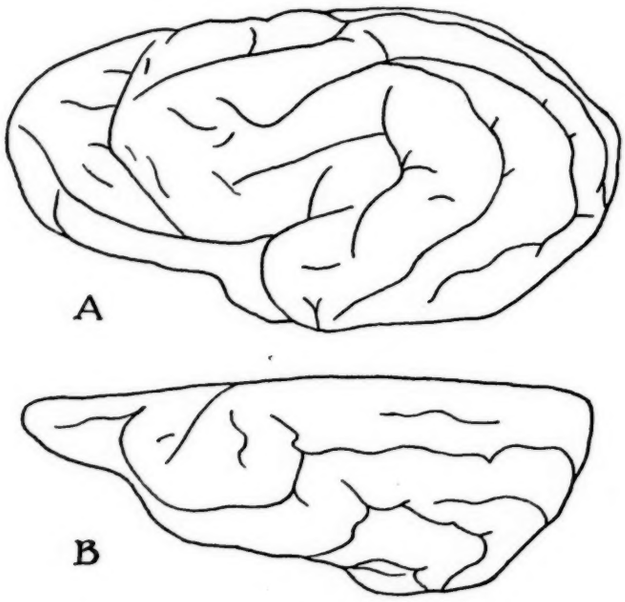

FIG. 37. Brain of a male wolf after Klatt (1921). 1/1. *A*. Left side. *B*. Left hemisphere of another brain from above.

high and broad, while the brain of a wolf (Fig. 37) is long, low and narrow. The same is true of the brain cases (Figs. 1 and 2). In the case quoted, the cranium of the dwarf type is brachicephalic, while the cranium of the wolf or wolfhound is dolichocephalic. But it must be borne in mind that the assumption of a more globular shape is due also to a considerable degree to the disappearance of the super-structures which, in form of supra-orbitals and nuchal crests, are of great influence in elongating the cranium and producing thereby its dolichocephalic character. The expansion of the brain case and the tendency to assume a globular form cause a widening of all the suprabasal parts, namely the erection

TABLE XXII

THE OCCURRENCE OF HUMAN PATTERN (CONTACT OF SPHENOID AND PARIETAL BONES : S.P.) AND ANTHROPOID PATTERN (CONTACT OF FRONTAL AND PARIETAL BONES : F.T.) IN RECENT MAN (AFTER ASHLEY-MONTAGU, 1933). CRANIAL CAPACITY ACCORDING TO R. MARTIN (1928)

Type	S.P. in %	F.T. in %	Capacity in cc	
			♂	♀
Mallicolese	27.5	68.9	—	—
New Caledonian	68.3	30.0	1420	1360
Javanese	76.4	23.4	1590	1396
Moriori	80.3	18.7	1455	1276
Andamanese	86.5	13.8	1281	1148
Australian	87.4	10.8	1310	1154
Veddah	84.6	9.0	1250	1139
Chinese	91.5	7.1	1456	1380
Indian	91.3	5.0	1345	1098
Maori	89.0	5.4	1476	1288
Marquesan	84.6	3.8	1427	1245
Burmese	98.0	1.9	1389	—
Eskimo	97.0	1.3	1563	1458
Amerindian	98.1	—	1440	—
Tierra del Fuego	100.0	—		
European*	97.6–98.5	1.5–2.4		

* According to different authors.

of the frontal bone, the rounding off and descending of the occipital bone, and the bulging of the parietal bones, particularly characteristic of the human brain case. These changes are also responsible for the reduction in thickness of the walls and for the retardation in suture closure, including the frequent persistence of the metopic suture in man.

I am inclined to bring another particularity of the human cranium into direct correlation with the expansion of the brain case, especially of its front part, namely the specific arrangement of the pterion sutures. It is well known that the frontal and temporal bones in man generally are prevented from coming into contact by the intercalation of the sphenoid and parietal bones which meet here directly; in anthropoids the reverse constitutes the rule, namely the frontal and temporal bones come in contact and the sphenoid and parietal bones are separated (cf. Figs. 8, *C* and 18, *B*). In lower primates the arrangement is

similar to that occurring in man, but not exactly the same. For more detailed information the reader is referred to Ashley-Montagu's (1933/34) exhaustive study on this subject. From this author's list it is apparent that considerable differences exist in the frequency of the "human" pattern among the various races of mankind. In the Amerindians and Europeans this type is almost universal, while the "anthropoid" pattern has been found in New Caledonians, Moriori, Australians, etc. from 10 to 30 per cent, in the case of the Mallicolese even up to 69 per cent. It is also apparent from the list that there is no connection between roominess of the brain case and the type of contact of the bones because in skulls with such a small capacity as the Veddah (1250 cc and 1139 cc, respectively) and the Andamanese (1281 cc and 1148 cc, respectively), the frequency of the anthropoid pattern is appreciably less than in the New Caledonians with a much larger capacity (1420 cc and 1360 cc, respectively). Yet this particular feature does not depend upon the absolute size of the cranial cavity but only upon the relative one, and this is the reason why most of the authors overlooked the point when discussing this problem. This may be deduced from the fact that, as already pointed out above, four of the five skulls (that is to say, 80 per cent) of pigmy chimpanzee known hitherto exhibit the human pattern in contrast to the common type of chimpanzee in which, according to Ashley-Montagu, this pattern

TABLE XXIII

OCCURRENCE OF THE "HUMAN" (S.P.) AND THE "ANTHROPOID" (F.T.) PATTERN OF THE PTERION SUTURES IN THE HIGHER APES (AFTER ASHLEY-MONTAGU, 1933)

Type	S.P. in %	F.T. in %
Hylobates	84.3	10.8
Symphalangus syndactylus	95.6	4.4
Pongo	67.7	25.3
Pan	1.2	95.8
Gorilla	1.0	94.7

is rather a rare occurrence (1.2 per cent). In gorilla the frequency of the human pattern is only 1.0 per cent. The orang-utang, it is true, shows a deviation. The human pattern recorded herein occurs in 67.7 per cent against only 25.3 per cent of the anthropoid pattern. It is true that this ape is not a dwarf type but its skull form deviates from that of the chimpanzee and gorilla by a remarkable erect position of the frontal bone.

In *Pithecanthropus* and *Sinanthropus*, as far as the pterion region is preserved, the human pattern already occurs but the contact zone between the sphenoid and parietal bones is extremely narrow, similar to the condition frequently observed in primitive types of recent mankind. The primary anthropoid type from which man evolved must have possessed the anthropoid pattern. I believe the more erect position of the frontal bone leaves room for the great wing of the sphenoidal bone to enlarge and extend upwards, meeting in this way the sphenoidal angle of the parietal bone. But the erect position of the forehead is, as shown above, one of the most characteristic effects of the expansion of the brain case. The human pattern of the pterion sutures, therefore, is in result of the relative or—in the case of man—absolute increase of the brain size. It is interesting to note that Lange (1924) and Hecker (1926/27) both proceeding from somewhat different standpoints,

arrived at similar conclusions. Lange (1924) supposed that the development of the frontal part of the brain case, possibly correlated with the shortening of the face, had something to do with the formation of the human pattern. According to Hecker (1926/27) the expansion of the brain case, especially in height and breadth, should be the responsible factor. This expansion should cause an elevation of the parietal bone, involving in particular its lower margin and sphenoid angle. The space thus vacated should be occupied by the great wing of the sphenoidal bone.

The question whether and how much the character of the pterion pattern in lower monkeys may be determined by still other factors remains open. But the behavior within the group of anthropoids, especially the surprising frequency of the human pattern in the pigmy chimpanzee in contrast to the normal occurrence, indicates that the increase in the size of the brain and the way in which its expansion affects the special arrangement of the constituents of the brain case must be considered as the real determinants of the specific human arrangement.

An excellent example to demonstrate existence and degree of eventual correlations between the size of the brain and cranial cavity and the size of the face is furnished by the proportions of the orbit. Adolph H. Schultz only recently (1940) called attention to it, in comparing the volume of the eye-ball with that of the orbit and the size of the body. We know from earlier studies by numerous authors (cf. R. Martin's textbook, 1928) that the ratio between the volume of the two orbits and the cranial capacity varies from 17.5 in Australian aborigines to more than 29 in Europeans, while it is only 7.2 in chimpanzee, 5.6 in orang and 5.3 in gorilla, or, in another way, the volume of the orbits in man amounts to 3.8 up to 4.6 per cent of the cranial capacity but to as much as 12 per cent in the chimpanzee, 13.3 per cent in the orang and 17.5 per cent in gorilla. The main reason for the differences between man and anthropoids is evidently due to the capacity of the human cranium being approximately three times greater than that of the anthropoids, while the volume of the human orbit is about the same as in the male chimpanzee and half the size of that of a male gorilla. But this is not all. Schultz came to the following conclusions: all the large primates possess proportionally much smaller orbits than is true of the small primates; among animals of the same species and age, the largest have proportionally the smallest orbits and vice versa; the relative capacity of the orbit is mainly dependent upon body size, regardless of genus, sex or age; the relative capacity of the orbit in recent man is second lowest within the entire primate group. The ratio between the volume of the eye and the capacity of the orbit varies among anthropoids and man between 17 in orang and 32 in man. The size of the orbit is dependent upon the size of the eyeball in a most general way only, the two structures varying to a surprising degree.

We may come to a better understanding of these relations by realizing that the size of the eyeball and the size of the orbit are determined by two different factors. The eye develops as a part of the brain in a very early stage at a time when the growth of the central nervous system exceeds all other organs. "Ontogenetically the eyes grow very rapidly in early life and extremely slowly in later stages of development" (Schultz, according to R. E. Scammon). The orbit, however, is constructed by skeletal elements which partly belong to the cranium and partly to the face. And even in the construction of the cranial portion, the super-structures, that is to say, the supra-orbitals take an active part. The disproportion between eye and orbit, therefore, must be less pronounced in fetal and

juvenile stages and acute in adults where the supra-orbitals and face have attained their definite size. That this really is so may be gathered from the figures supplied by Schultz.

Table XXIV shows the size of the eye in percentage of the size of the orbits for chimpanzee, orang and man (negro) in the different stages of development. In the adult anthropoids, in which the face is greatly enlarged in relation to the cranium, as shown above, the eye occupies only a small portion of the orbit (17.2 to 25.2 per cent), while in man its share is much greater (38 per cent), almost twice as much because of the relative smallness of the human face. Independently of this general correlation between eye and cranium and orbit and skull, there are other factors which influence the degree of correlation as, for instance, the absolute size of the eyeball which is largest in chimpanzee and smallest in orang. Yet, all this may be disregarded since it has no direct bearing on the problem discussed herein.

TABLE XXIV

ONTOGENETICAL CHANGE IN SIZE OF THE EYEBALL IN PERCENTAGE TO THE SIZE OF THE ORBIT (AFTER A. H. SCHULTZ, 1940)

	Chimpanzee	Orang	Man
Fetus ♀	92.1	—	75.5
Newborn ♀	57.6	64.3	45.0
Infant ♀ ♂	41.0	45.6	—
Juvenile ♀ ♂	34.5	29.1	—
Adult ♀	25.2	18.2	M + F } 38.0
Adult ♂	21.4	17.2	

The topographical relation of the orbit to the brain case also undergoes a characteristic change in the course of human evolution which in turn distinctly demonstrates that the orbit is part of the face. I have already pointed out this fact in an earlier publication (1939 b; III). As Fig. 38, *A*, shows, the orbit in chimpanzee is overlapped by the brain case only in its posterior portion and correspondingly the roof formed by the far-projecting supra-orbitals. In man, however (Fig. 38, *C*), the brain case expanded to such an extent as to have caused the disappearance of the supra-orbitals and the orbit now underlies the entire brain case. *Sinanthropus* (Fig. 38, *B*) also in this regard represents an intermediary stage. This transfiguration makes evident that the orbit as a constituent of the face retained most of its original position, while the brain case because of its enlargement in volume takes active part in the alteration of the topographical relation between the two structures. Such behavior is in complete accordance with the general conditions found in large dogs, on one side, and dwarf dogs, on the other, as a comparison of Fig. 38 with Fig. 4 will demonstrate. Strange enough, Bolk (1923) uses the fact that the orbit is located under the brain in man and before the brain in anthropoids as an argument against any closer relationship existing between the two groups. If his conclusion should be correct, then the King Charles spaniel would have nothing in common with an Irish wolfhound.

It was shown above, that a close correlation exists between the size of the brain case and the size of the face: the larger the former, the smaller the latter and vice versa. Since the jaws are the essential constituents of the face, a large face implies the development of a large and strong masticatory apparatus. In correspondence therewith, the apparatus

requires strong buttresses on the part of the cranium as a counterbalance against the chewing force, and simultaneously a large surface for the attachment of the chewing muscles, especially for the temporalis. If the brain case is relatively small as in the case of large jaws, the surface available is not extensive enough to meet that requirement. In consequence thereof, the super-structures are developed so as to strengthen the bone and, at the same time, to enlarge the surface.

That the development of the sagittal and occipital crests of the anthropoids is closely correlated to that of the temporal muscles was realized long ago by Waldeyer, Ranke, Selenka and Poirier. Matiegka (1906) contributed a special study to those formations. He describes their occurrence in various groups of mammals and concludes that the size of the animal cannot be made responsible for their development because of their occurrence also in small animals. Unfortunately, Matiegka completely failed to realize the existence of the correlation in question; otherwise he would have known that the formation of the

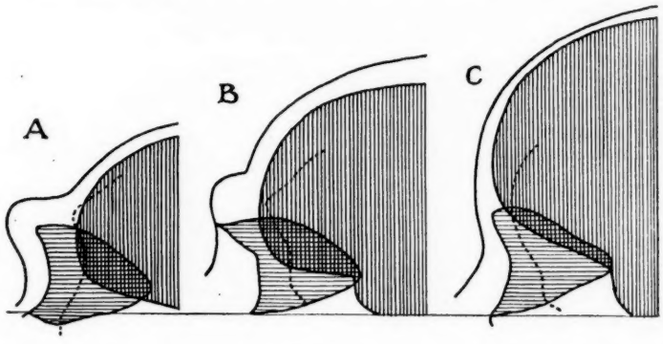

FIG. 38. The topographical relation between the orbit and the frontal part of the cranial cavity in a male chimpanzee (*A*), a female *Sinanthropus* individual (*B*) and a modern male North Chinese (*C*).

crests is not a mere question of body size but one of relative size. Mollison (1919), confining his studies to primates, ascertained the development of the crests as being dependent upon the size of the brain case which in turn is dependent upon the size of the brain and the development of muscles attached to the surface thereof; in those animals which are small but have relatively large brains, the crest fails to develop. Mollison computed a cavo-temporal index, that is, the relation of that surface of the brain occupied by the temporal muscle to one face of a cube representing the volume of the cranial capacity. This index totals 55 in man and 182 in gorilla. In the examples of dogs given herein, it comes to about 60 in the King Charles spaniel and about 218 in the Irish wolfhound.

The majority of authors refer to the crests merely as being conditioned by the mass of the temporal muscles and the size of the cranium. There is no room for doubt, however, that the supra-orbitals must also be placed in a similar category. Görke (1904) was first to discover that the development of these structures depends upon the strength of the chewing apparatus as well as upon the degree of the slanting of the forehead which in turn serves as an indicator of the brain size. The author describes under the name of crista canina and crista alveolo-zygomatica the well known beams of compact bony substance which arise on either side of the alveolar process from the canine and molar regions and course upwards toward the nasal-frontal and the fronto-zygomatic junctions where

they merge in the supra-orbital tori. These tori serve as buttresses against the force of mastication. According to Strasser (1913) the conditions in man are the same in principle. He distinguishes two pillars within the construction of the facial frame serving to transfer the chewing force to the base of the cranium. One of them, the frontal pillar, is represented by the nasal bone and the frontal process of the maxilla, the other, the zygomatic pillar is located within the posterior lateral wall of the orbit. In a comparative study of the supra-orbitals Toldt (1914) accepted Görke's interpretation and others followed him. Only Aichel (1914) advocated the absurd contention that the supra-orbitals of the apes were due to the effect of the corrugator supercilii. This muscle, stimulated by the exaggerated activity of the mimical muscles, should irritate the periosteum and cause the underlying bone to proliferate.

It cannot be doubted, however, that the formation of the supra-orbitals must be considered a consequence of the construction of the skull and of the special arrangement of its two constituents, the cranium and the face. When the face takes its position more or less before the cranium, there is evidently a static and dynamic impulse to strengthen the superior parts of the face by forming projecting structures which have to serve as transmitters or buttresses, especially in cases in which the dentition and masticatory apparatus are strongly developed. If, however, the face has been reduced and more or less underlies the cranium, such protruding formations are no longer required, for the cranium itself is then strong enough to serve as an adequate recipient.

As noted above, there is a close relation between the frontal super-structures and frontal sinuses. In large dogs (Figs. 1 and 4, *C*) the space between nasion and anterior pole of the cranial cavity is occupied by a large sinus on either side. In dwarf dogs, however, the cranial cavity extends forward up to the nasion, the sinus having disappeared completely. Coolidge (1933) demonstrated with the aid of skiagrams (see above) that a frontal sinus is lacking in pigmy chimpanzee, contrasting remarkably to the regular type. In a special study on the frontal sinuses Weinert (1926, 1928) already in the title designates the sinus as a phylogenetic character. He concludes that they may develop in certain cases but are of no functional importance. If they do exist, however, they should be hereditary, a quality Weinert considers absolutely inseparable from any structure of phylogenetic importance. Since that author found that the frontal sinuses were well developed in Dubois' *Pithecanthropus* Skull I, while missing in gibbon skulls, he deduced that *Pithecanthropus* could not have been a giant gibbon as was claimed by Dubois. This case is an interesting example to demonstrate the incorrectness of conclusions, seemingly cogent, if based on insufficient understanding of the true character of the structures. There is no question today that *Pithecanthropus* is a genuine hominid and not a gibbon but this fact cannot be proved on the basis of Weinert's argumentation. As early as 1924 (1924, a) I was able to demonstrate, in agreement with Strasser (1901), that the formation of the sinus must be regarded as a consequence of the architectonic structure of the face. The essential components of the face comprise structures completely differing in shape and location—namely, from below to above—the plate-like palate with the horseshoe-shaped alveolar process holding the teeth, the nasal tunnel, the funnels of the two orbits and, finally, the ovoid capsule of the brain. These structures are welded on to one frame and strengthened by the frontal and zygomatic pillars mentioned above, but since their outlines do not conform, large interspaces remain between them which are of no static or dynamic

significance in the architectonic construction of the face. In other parts of the skeleton, particularly in long bones, those spaces are occupied by marrow. Within the face, however, they are in immediate contact with the respiratory tract and can, therefore, become filled with air. The larger the individual elements of the face, the greater, of course, is the incongruity between them and the larger the interspaces, that is to say, the sinus. In the case of the frontal sinus the topographical relation between face and brain case also plays a decisive rôle. If the orbits take their position far in front of the anterior pole of the brain case, as in large dogs or in gorilla and chimpanzee, the interspace between orbit and brain case is occupied by a large sinus (cf. Figs. 4 and 5, *C;* 7, 29, 38), while in those where the orbits underlie the brain case the sinus is reduced or completely missing (cf. Figs. 4 and 5, *A;* 29, 38, *C*). In man the sinus shows a great variability and is not infrequently completely missing. It must be borne in mind, however, that the existence or absence of the frontal sinus apparently also depends upon other factors difficult to analyze in each case. As a matter of fact, the sinus is rather large in forms in which brain and brain case are relatively small in proportion to the entire skull, while it is absent or reduced if the brain and brain case are relatively large.

The orang occupies a special place with respect to the development of the supra-orbitals and the frontal sinus. The supra-orbitals are not particularly projecting and the sinus is missing. The required support of the frontal region here has been obtained by extreme annular thickenings of the orbital rims which directly join the frontal and zygomatic pillars. Neither space nor frontal sinus is required. This particular arrangement seems to be dependent upon the special form of the brain case which is much more globular in orang than in gorilla and chimpanzee.

Development and size of all super-structures of the cranium, supra-orbitals as well as crests, are contingent only upon the development of the masticatory apparatus and the topographical relation between cranium and face. They are superposed on the brain case and only indirectly influenced by the size of the brain, inasmuch as relatively small brains and correspondingly large jaws induce large super-structures, while large brains and small jaws render them almost superfluous. Numerous investigators studying the relation between brain, brain case, and temporal muscles made the mistake in assuming that these muscles were capable of exerting a direct pressure on the brain case and could thus prevent its expansion. Anthony (1906), for instance, considered the supposed compression of the brain case produced by the joint action of the two temporal muscles as the immediate cause of the relatively small volume of the brain of the carnivores in contrast to that of the primates. In order to prove the correctness of this conception, he removed the temporal muscle of one side from very young dogs and subsequently compared the altered conditions with those of the normal side. The only real change he could observe, however, was the turning of the sagittal crest toward the operated side, a process very easily understood, since the formation of the crest depends entirely upon size and extension of that muscle. In addition, Anthony noted that the bone of the operated side was thicker and its outer surface rounder than that of the normal one. This condition may also be adequately explained by the absence of the muscle. But Anthony's own illustrations show that there is not the slightest indication of any alteration of the interior surface of the brain case. Anthony even ventured to assert that the extraordinary expansion of the human brain was made possible only by the reduction of the chewing apparatus and that

this in turn prevented the temporal muscles from covering the entire cranium and thus submitting its contents to a strong outside pressure. Fick (1857), who carried out the same experiment long before Anthony, recorded in agreement with this author, that the force of the temporal muscle of the normal side alone impelled the sagittal crest to move towards the operated side but he strongly emphasizes that the brain case as well as the brain did not exhibit any alteration. According to Anthony's view, the primary determinant factor in the special development of the human brain is the reduction of the masticatory apparatus, while in reality the reverse holds true: the muscles of mastication are not capable of exerting any influence upon the formation of the brain but there is a close growth correlation between brain and brain case, on one hand, and the masticatory apparatus, on the other, as stated above.

The question whether the brain or its bony sheath may be responsible for the special shape of the cranium is also reflected in the old controversy on the cause of pathological forms of the human cranium like scaphocephaly and similar deformities. For further details of this particular problem, the reader is referred to Mijsberg's recent publication (1932) in which the pros and cons are discussed. Bolk (1915, 1919 and 1921) contests the correctness of Rudolf Virchow's theory, according to which premature obliterations of the sutures produce such deformities. But by considering this closure as an atavistic phenomenon, Bolk seems inclined to follow those authors who regard the brain case and not the brain as the decisive factor in the development of the deformities. Mijsberg is more precise in this respect. He concluded that the obliteration of sutures could in no instance produce abnormal cranial forms, the premature closure merely representing the expression of a fixation of abnormalities already in progress. Although Mijsberg's formulation is not exactly in answer to the fundamental question, his criterion moves the argumentations of the numerous supporters of Virchow's theory in favor of those who credit the brain with the real initiative in producing the abnormalities in question. That there is a strict correlation between brain, brain case and face with the brain as the determinant factor may be proved in a rather impressive manner by the study of microcephalic skulls. Mollison in 1926 examined a living microcephalic individual, whose cranial capacity was estimated to amount to about 1000 or 1100 cc. A heavy fall on the head in patient's early youth seems to have prematurely stopped the growth of the brain. The main characteristics of the cranial deformity of this case consist of a low brain case, a flat and receding forehead, far projecting supra-orbitals and very spacious frontal air sinuses as shown by skiagrams. Mollison considers this case a natural experiment demonstrating the manner in which the cranium alters its form if the proportion between brain case and its contents undergoes a change. The fact that the cranium assumed the aspect of that of a Neanderthal type, that author interprets as proof that its form and most essential features are not dependent upon specific relationship but rather upon the dynamic effect of the disproportion in size between brain case and brain.

My own attention was drawn to this rather promising problem when coming across a microcephalic skull in the anthropological collection of the Musée d'Histoire Naturelle in Paris. I am greatly indebted to Dr. Paul Rivet who very kindly placed this specimen at my disposal for closer examination several years ago. In the course of my study, it became apparent that it would be advisable to include also those microcephalic specimens made known over seventy years ago (1867) by Carl Vogt's famous treatise on the "Ape-

Man." Due to special circumstances, I have, as yet, not been able to publish this study in extenso; the main results, however, were summarized briefly in an abstract of a lecture on this problem (1932). The microcephalic specimen I selected from the Paris museum is of some historic interest. It was already referred to and reproduced in Gall and Spurzheim's work on the anatomy of the nervous system (1810, Atlas, Pl. XX) and originally belonged to Gall's private collection. This microcephalic skull is that of a girl of approximately 20 years of age, labelled as "completely imbecile." The most astonishing peculiarity of this skull is not so much the smallness of the brain case and its special form but the relative size of the face and the pronounced prognathism. Fig. 39, *A* and *B*,

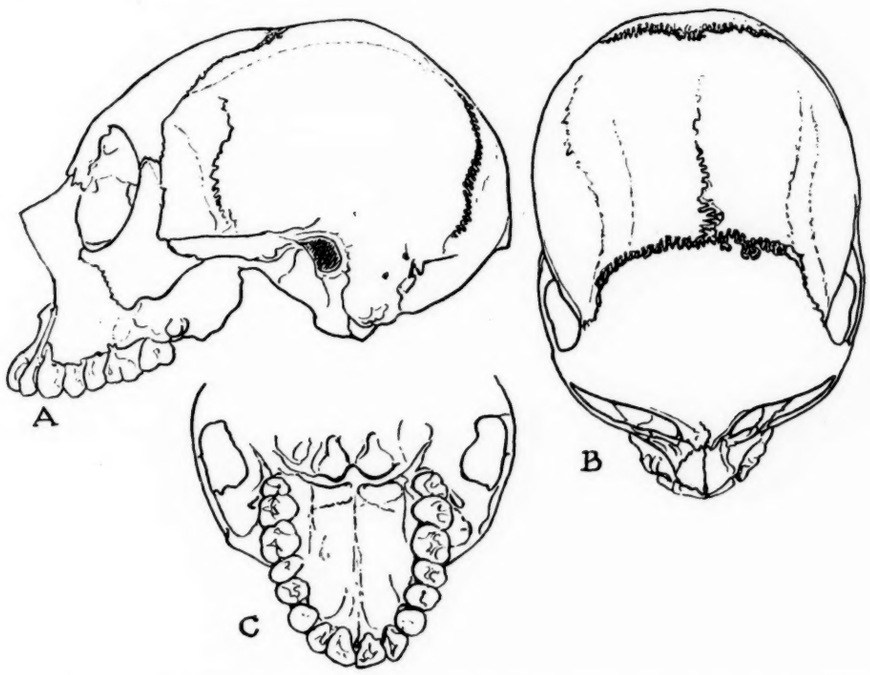

FIG. 39. Skull of a microcephalic Parisian woman. Coll. Mus. d'Hist. Nat., Paris, no. 5503. 5/12. *A*. Lateral view. *B*. Vertical view. *C*. Palate and dental arch.

illustrates the skull in lateral and vertical views. The forehead is flat and strongly receding; the greatest breadth of the skull coincides to the biauricular plane; there is a pronounced postorbital constriction and the temporal line courses far above in the vicinity of the midline. All these features characterize primitiveness; typical supra-orbitals are not developed but the orbit comes to lie considerably before the cranium. The face shows a marked degree of total and alveolar prognathism, the upper jaw is high and the zygomatic arch bridges over the temporal fossa to a considerable distance from the cranial surface, a consequence of the smallness of the brain case. The palate and dental arch (Fig. 39, *C*) are relatively long and narrow.

Before discussing the significance of these peculiarities, we refer to a second case of microcephalic skull rather similar to the first one, the cast of which is contained in the collection of the American Museum of Natural History. This skull was described by

Dru-Drury (1919/20) as belonging to a Basuto woman 32 years old. According to Dru-Drury, the woman was built like a child of 12 years, weighing 60 lbs. As Fig. 40 shows, the cranium is almost identical with the Parisian specimen but it is lower, longer and relatively narrower and the postorbital constriction is still more pronounced than in the first case. Supra-orbitals are missing but the temporal line courses rather close to the midline. The relatively large face reveals a marked degree of total and alveolar prognathism. The nasal bridge, however, is much flatter and the length and narrowness of palate

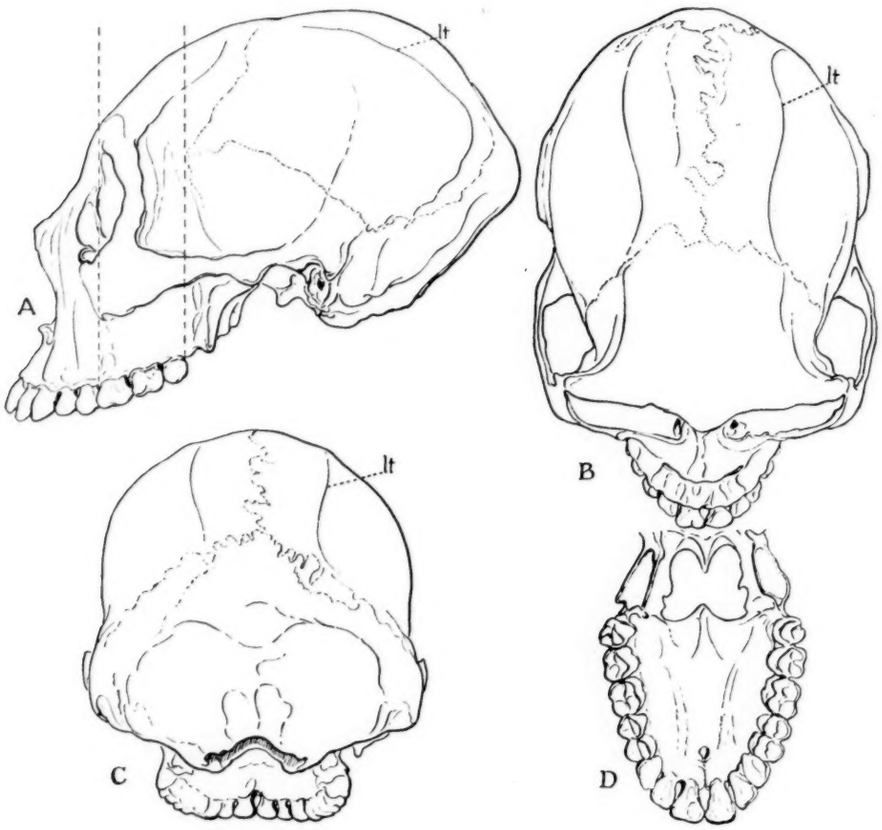

FIG. 40. Skull of a microcephalic Basuto woman (cast). 1/2. *A*. Lateral view. *B*. Vertical view. *C*. Occipital view. *D*. Palate and dental arch.

and dental arch are still more developed than in the Parisian skull. If we disregard the differences outlined which may be partly accounted for as racial, the skulls are strikingly similar in principle.

In addition, a third skull is illustrated in Fig. 41 already described by C. Vogt. This skull belongs likewise to a woman of about the same age as the Negro but is of European race (Margarete Maehler, 33 years old). The illustration shows the same smallness of the cranium, the relative size and strong prognathism of the face and, in contrast to the two skulls first described, heavy supra-orbitals separated from the forehead by a distinct and broad depression. This region lodges a large frontal sinus. The topographic relation

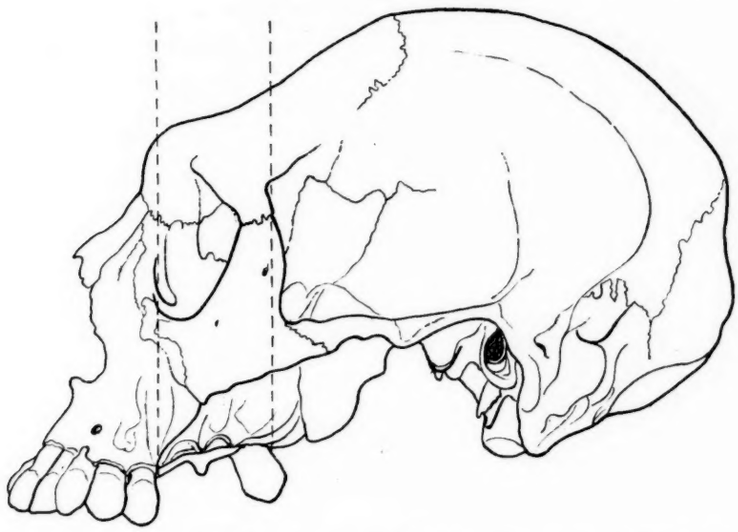

FIG. 41. Skull of the microcephalic Margarete Maehler after C. Vogt (1867, Pl. 19). 2/3.

between brain case and face can best be illustrated by a median section like the one reproduced in Fig. 42. The skull concerned belonged to a microcephalic male individual of European origin—Conrad Schüttelndreyer, 31 years old—also described by C. Vogt. The face, rather large in proportion to the size of the brain case, is not located below the latter as under normal conditions (cf. Fig. 29) but before it. The region of the supra-orbitals which, as in a gorilla (cf. Fig. 29), is located completely in front of the anterior pole of the cranial cavity in this case also lodges a large air sinus. Furthermore, it is of great interest

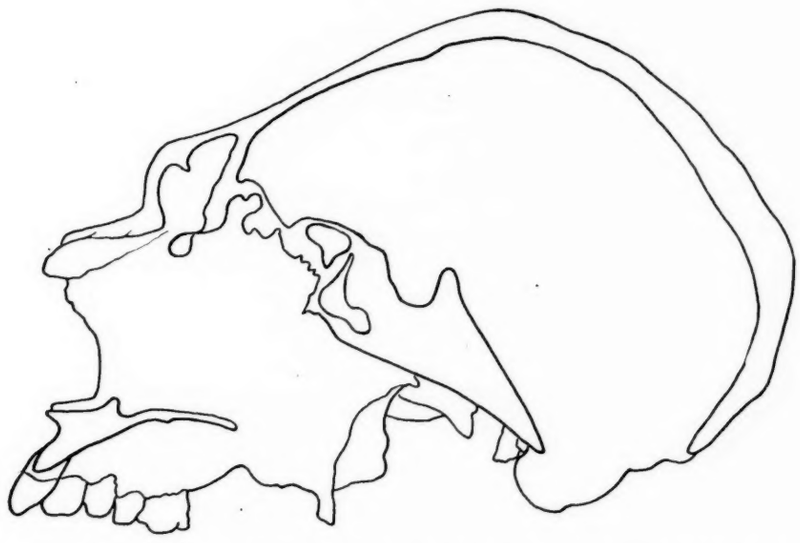

FIG. 42. Median section through the skull of the microcephalic Conrad Schüttelndreyer after C. Vogt (1867, Pl. 11). 2/3.

that there is no indication of a deflection of the cranial case as is characteristic of man but that its axis forms a perfectly straight line as in gorilla (Fig. 29). In accordance with such a configuration and position of the brain case, the aperture of the foramen magnum opens directly downwards and not forwards if the skull is orientated in a Frankfort plane.

From the measurements listed in Table XXV, it may be gathered that all four microcephalic skulls belong to young adult individuals but the cranial capacity of none of them exceeds 365 cc (average 317.5 cc). This is not quite one-quarter of the average capacity of recent man, even less than the average for chimpanzee (396 cc).

The ratio between endocranial length and total length of the skull (*op-pr*) varies from 62.4 to 70.2. Table XIX makes it evident that this ratio under normal conditions reaches 80–90, while in *Pithecanthropus* it is only 70. The ratio of the height of the face to the

TABLE XXV

MEASUREMENTS AND INDICES OF MICROCEPHALIC SKULLS

Origin	Sex	Age	Capacity in cc	Total Length (*op-pr*) in mm	Endocranial Length in mm	Facial Height (*n-pr*) in mm	Index of 3 and 2 $\frac{3 \times 100}{2}$	Facial Angle	Index: Facial and Endocranial Length $\frac{4 \times 100}{3}$	Max.-Alveolar Index
			1	2	3	4	5	6	7	8
Parisian	♀	20	280	154	101.5	53.0	66	73.5°	52.2	109.2
Negro (Basuto)	♀	33	340	154	108.0	64.0	70.2	74.0°	59.2	110.5
Germany (M. Maehler)	♀	33	285	155	97.0	73.0	62.4	78.0°	75.2	94.2
Germany (C. Schüttelndreyer)	♂	31	365	167	115.0	57.5	69	67.0°	50.0	107.5
Average		29	317.5	157.5	105.4	61.9	66.9	73.1°	59.15	105.3

endocranial length varies in microcephalics from 50 to 75.2. In normal human skulls it reaches 44 and in *Pithecanthropus* 55.0. The prognathism with an average degree of 73.1 for the profile is much more pronounced than in normal man, even compared with races showing a marked degree of prognathism and taking into account that three of the microcephalic individuals are Europeans, for according to Lüthy (R. Martin's textbook, 1928) the average facial angle varies from 76.8° (Australian natives) to 87° (Swiss). The maxillo-alveolar index with an average of 105.3 indicates that palate and dental arch are very narrow, the European average amounting to 113–117 and that of all human races from 108 to 126 (following R. Martin).

The microcephalic skulls exhibit as a whole and in certain details remarkable "anthropoid" characters; the cranium is small in relation to the entire skull, while face and masticatory apparatus are not reduced proportionally. Fig. 41 shows the row of the upper molars underlying the supra-orbital region as in gorilla (Fig. 24, *A*), differing markedly in this respect from the conditions in normal man (Fig. 24, *C*). The consequences of such a disproportion are the projection of the face, that is to say, its situation in front of the brain case, the flattening of the forehead, the development of the supra-orbitals or their equivalent combined with large frontal air-sinuses, the pronounced postorbital constriction, the plane of the mastoid region representing the greatest breadth of the cranium (cf. Fig. 40,

C, with Figs. 26, *C*, and 20, *A*) and finally the course of the temporal lines approaching rather closely the sagittal suture. In respect to the closure of the cranial sutures the four skulls differ from one another. In the Parisian skull the obelion and lambda portion of the sagittal suture and the greatest part of the squamosal suture are closed. In Skull Schüttelndreyer the sagittal suture is obliterated, while in Skull Maehler all sutures are still patent. It is impossible to judge the conditions in the Basuto Skull since the cast is not reliable in this respect and Dru-Drury failed to mention it in his description. As much as may be gathered from the data available, it seems that there is no distinct tendency toward prematurely closed sutures. As to the upper jaw, the relatively long and narrow palate and dental arch correspond to what may be expected of an anthropoid-like form. The teeth are relatively large but their patterns do not show essential deviations from the norm.

Compared with the microcephalic case described by Mollison the four skulls differ characteristically in form and relative size of the face. But it should be borne in mind that Mollison's specimen has a cranial capacity of 1000 to 1100 cc, while the four cases referred to show a capacity of only one-third of this and, on the other hand, in the first instance the development of the deformity occurred in early youth, whereas the microcephaly in the other cases was inborn. That anthropoid characters of microcephalic skulls are more pronounced the smaller the cranium, follows distinctly from Vogt's figures and illustrations to which the reader is referred.

Vogt considers microcephaly as a partial atavism which primarily affects the hemispheres of the cerebrum. As an essential consequence thereof, the normal ontogenetic development should divert in such direction that the characteristics of the stem from which man evolved become reproduced. In other words the microcephalics have to be interpreted as genuine reversions to ancestral forms, hence the title "ape-man" of Vogt's publication. Mollison, on the other hand, denies that phylogenetic relation determines the configuration of the skull which should depend only upon dynamic effects caused by the disproportion between brain case and brain.

In the preceding chapter, I was able to prove that there exists a direct correlation between sizes of brain and brain case on one hand, and face on the other; the larger the brain and the brain case, the smaller the face and vice versa. In anthropoids and large dogs the brain is small in relation to the size of the body and the size of the entire skull, while the face, especially the masticatory apparatus is very large. In man and dwarf dogs exactly the reverse conditions exist. In human microcephalics the growth of the brain became arrested in an early stage of ontogenetic development; the brain, therefore, remained small, while the growth of the face continued, not at the same rate as under normal conditions but less impeded than is true of the brain. Fig. 35 demonstrates the degree of these conditions. The microcephalic skull (– –) in cranial size ranges between chimpanzee and *Pithecanthropus* Skull IV, but in size of its face between *Pithecanthropus* and Neanderthal man. The ratio between the volume of its face and of its cranial capacity (Table XXI) amounts to about 66 against 26 in normal man, 100 in *Pithecanthropus* and 207 in gorilla.

The arrested growth and the differentiation give the microcephalic skull the form characteristic of all such types in which the brain is small and the face large. Since the special form and the special features developed on such a basis are not in the least specific

to anthropoids but also occur in other mammals under the same special conditions, microcephalic peculiarities cannot be interpreted as being "atavistic." The fact that the microcephalic skull bears a similarity in many respects to that of anthropoids is due to two circumstances, namely (1) that the basic character of the entire human construction is simian and (2) that the living great apes are also represented by forms with small brains and large faces. Microcephaly thus only serves to demonstrate that the correlation between brain and face is of a general biological character and that even a seemingly fixed status in the course of evolution may be reversed if its basic conditions change.

Vogt believed that the brain of microcephalics in certain proportions also shows a resemblance to that of the anthropoid. The form and proportions of the brain of the Basuto woman, however, as much as can be defined from the endocast, fail to show any appreciable differences when compared with the normal human brain (Fig. 43). The brain

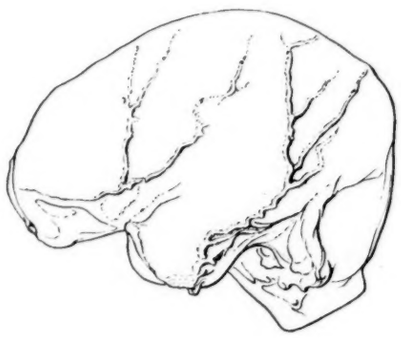

FIG. 43. Endocast of the skull of the Basuto woman of Fig. 40. 1/2.

is even surprisingly high within the parietal region, in fact considerably higher than the brain of *Sinanthropus* and *Pithecanthropus*. The only primitive characters are the lowness of the frontal lobe and the pronounced keel-like formation of the orbital surface, both features apparently representing adaptations to the special form of the brain case in the zone of contact with the facial skeleton. To what extent even certain characteristic details are conditioned by the special development of other structures is illustrated by the pattern of ramification of the meningeal vessels. In an earlier publication (1938) I was able to show that the distribution of the middle meningeal artery in man follows two patterns: in primitive man, especially in *Sinanthropus*, the main branch is represented by the posterior ramus, whereas the anterior one appears as the insignificant terminal branch. Moreover, the entire system of ramification is scanty. In man, however, the anterior ramus has developed into the principal vessel and the entire ramification has become abundant, while the posterior ramus has been reduced to a side branch. The endocast of the Basuto skull shows a large posterior ramus and only a faintly indicated anterior one with the entire system of ramification poorly developed. This pattern corresponds to primitive conditions such as observed in *Sinanthropus* Skull II Locus L, for instance, (cf. 1938, Table I, Fig. 3). The type of distribution of these vessels does not depend upon the size of the brain but upon the size of the cranial bones which in microcephalics are reduced to conform to the brain.

The kind of lesion responsible for arresting the brain growth and producing microcephalic conditions is not known. It seems that there must be some deficiency in the general "anlage" material of the central nervous system which may be exhausted earlier or later after a certain period of growth. The specific human character of the type as such, however, does not undergo any alteration as is proved by the mask of the Parisian woman (Fig. 44) also reproduced in Gall and Spurzheim's Atlas (1810, Pl. XX). Eye, nose, lips

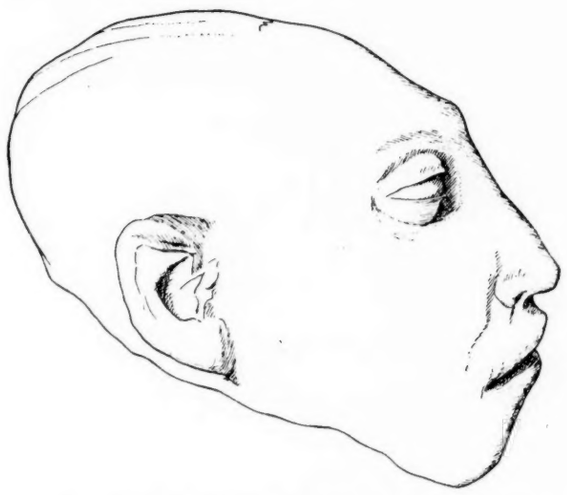

FIG. 44. Head of the microcephalic Parisian woman of Fig. 39, after a drawing in Gall and Spurzheim's Atlas (1810, Pl. 20). 1/2.

and ear resemble in all parts those of normal-sized women, with no sign of "atavism" but the specific microcephalic forms and proportions of cranium and face remain unchanged, in spite of the normal appearance of the soft parts. This behavior shows once more that it is really only the relation between the size of the brain and the size of the skull which determines the special configuration of the microcephalic skulls.

V. Brain-Size and Body-Size and their Determining Factors

The biological law underlying the correlation between cranium and face rules that small animals have large brains in relation to their body-size, and large animals small brains. If no other material but skulls are available for the interpretation of their morphology, the only equivalent to the size of the brain is represented by the cranial capacity. As an equivalent to the body-size may pass, for want of something better, the size of the entire skull, which in turn is determined either by its weight or—not as precisely but better controllable—by its total length. Since the latter, however, is a linear measurement, the cranial capacity must be substituted by a corresponding gauge, the greatest interior length of the brain case appearing to be the most adequate one.

If the respective weights of the brain and body are represented, their correlation is easily and impressively demonstrated without showing any appreciable change in principle. The first to deal with this problem were Brandt (1898), Dhéré and Lapicque (1898 a, b, c), and E. Dubois (1898) who made use of weights and calculated the ratio between brain-size

and body-size on that basis. Their lists show that smaller animals have much more brain compared with body-weight than large animals. Weber's computations (1897) listed in Table II show the same: small platyrrhine monkeys lead with a ratio of 1 (brain-weight) to 17–27 (body-weight), while orang and gorilla stand at the end with a ratio of 194 and 400, respectively. Dubois computed this ratio for man at 46 for males and 42 for females. He even ventured further by attempting to find a formula with which the degree of intelligence (psychical factor) in some way bound to the quantity of the brain, could be determined. This quantity has a certain relation to the surface of the body and the degree of the relationship can be expressed by the relation-exponent r. According to the formula

$$r = \frac{\log E - \log e}{\log S - \log s}$$

in which E and e stand for brain-weights and S and s for body-weights of two animals of the same or at least closely related species but of different size. By means of the exponent r Dubois computed the "cephalization coefficient" k on the basis of the formula

$$\log k = E - r \log S.$$

In man, for instance, r, as in most of the other mammals, should equal 0.56 and k 2.822 in males and 2.818 in females, whereas the latter coefficient amounts to only 0.395–0.493 in marmosets and to 0.753 in orang. The author thus considers k a mathematical expression of the special cerebral and psychical organization of the animal concerned.

According to Julian Huxley (1932), the relation brain-weight and body-weight follows entirely the elementary law of relative growth and Dubois' formula can, therefore, be expressed also in the following way:

$$y = bx^k \text{ or } \log y = \log b + k \log x.$$

y in this formula means the magnitude of the differentially growing organ, in our special case the brain-weight. x means the magnitude of the animal, in our case the body-weight. k corresponding to Dubois' relation-exponent r is the growth-partition coefficient of the brain and b, corresponding to Dubois' cephalization coefficient k, the fractional constant in the growth-partition formula. In a later publication (1937) with Teissier, Huxley replaced r or k by α now called "equilibrium constant" and b, the fractional constant, is defined as "initial growth index." The new heterogonic or allometric formula, which means that the growth of an organ differs from that of the body, is written as follows:

$$y = bx^\alpha,$$

and using Dubois' original terms and symbols as follows:

$$E = kS^r,$$

or thrown into logarithmic form

$$\log E = \log k + r \log S.$$

When plotted on a double logarithmic scale, the diagram forms, instead of a curve, a straight line, the value of which is determined by the slope of the line, the equilibrium constant (r) indicating the relative size of the increments while the initial growth index b (k) expresses the value of y (E) when x (S) equals one. In the three examples of primates

given above, man shows a four times greater initial growth index than orang and about seven times greater than marmosets. But it is rather questionable whether this method can really be used for obtaining objective and reliable figures helpful in estimating the magnitude of the "psychic factor."

In his list of animals in which the ratio of brain-weight to body-weight is recorded, Dubois (1914) also refers to *Canis domesticus* with a ratio of 199 based on a brain-weight of 87 g and a body-weight of 17,300 g. As has been shown above, the species *Canis domesticus* includes such a large number of variations or races of different sizes, as to render Dubois' estimations worthless. To find the real relations, Lapicque (1907) took the precaution of arranging adult dogs according to races and sizes in ten different groups, and determined body-weight and brain-weight of each dog. Table XXVI records his findings.

TABLE XXVI

BRAIN-WEIGHT AND BODY-WEIGHT OF 10 DIFFERENT GROUPS OF DOGS ARRANGED ACCORDING TO SIZE, AFTER LAPICQUE (1907)

Number of Specimens	Group	Average Body-Weight in g	Average Brain-Weight in g	Ratio
17	I	38,000	107	355
27	II	28,000	95	295
27	III	22,000	94	234
18	IV	19,000	86.5	219
27	V	15,000	85	176
27	VI	10,000	75	133
24	VII	7,000	72	97
11	VIII	5,000	64	78
6	IX	3,000	60	50
4	X	1,600	51	31

It follows from these figures that in group IX and, especially group X comprising dwarf dogs, the ratio is seven to ten times higher than in group I with the largest dogs. The equilibrium constant for the dog computed from these figures, according to Lapicque, is not 0.56 as claimed by Dubois to be valid for all mammals but 0.23 or 0.26 after Klatt (1913, 1921), which corresponds to an "initial growth index" for the dog's brain of 6.07 against 0.368 in Dubois' list. If 0.56 should be the correct equilibrium constant for man and 2.82 his initial growth index, the dog's index would double that of man. But the equilibrium constant of the anthropoids, including man, is not at all 0.56 or 0.5493 (Dubois, 1898). Dubois based his calculations on the comparison of orang as representing the largest anthropoid and siamang the smallest. When, however, man is compared directly with chimpanzee—quite as justifiable as the comparison of orang and siamang—$r(\alpha)$ equals 1.32, according to the formula (cf. above):

$$r(\alpha) = \frac{\log E - \log e}{\log S - \log s}$$

when the following figures are derived for brain-weight (E) and body-weight (S) of man: 1375 and 63010 (after Dubois), and for brain-weight (e) and body-weight (S) of chimpanzee:

345 and 22045 (after Bonin, 1937). From $r(\alpha) = 1.32$ the initial growth index of man k (b) amounts to 0.00636 and not 2.82 (Dubois). But in a later publication (1898 b) Dubois derived quite a different value for $r(\alpha)$. At this occasion he made use of Ammon's material comprising measurements of German recruits. He divided the material into four groups, arranged according to the height of the body and from the height calculated first the average weight of the body and then from the length and breadth of the head (using Welcker's method) the cranial capacity and the brain-weight, respectively. Table XXVII contains the results derived by Dubois. It goes without saying, that a calculation based merely on such uncertain computations must be accepted with the greatest reservation. But $r(\alpha)$ defined by Dubois in such a questionable way equals 0.25—that is to say, it is rather close to Lapicque's figure for dogs (see above)—and not 0.56, and k (b) computed on the basis of $r = 0.25$ totals 86.8 for males and 81.7 for females instead of 2.822 and 2.818, respectively, as claimed by Dubois (1914).

TABLE XXVII

DUBOIS' (1898 b) CALCULATIONS OF BRAIN-WEIGHT AND BODY-WEIGHT ON THE BASIS OF AMMON'S FIGURES OBTAINED FROM MEASUREMENTS OF GERMAN RECRUITS

Group	Average Body-Height in cm	Computed Body-Weight in kg	Computed Cranial Capacity in cc	Computed Brain-Weight in g	Ratio
I	177.4	72.74	1525	1430	51
II	171.9	67.49	1486	1388	49
III	165.7	60.11	1452	1351	44
IV	159.5	55.50	1436	1333	41

Our understanding derived hereby about the "psychical factor" is certainly not much more than what was known hitherto, namely that the brain of man comprises considerably more cerebral substance than the brains of orang or marmosets. But we are not so much interested in Dubois' cephalization coefficient as in the simple relation between brain-weight and body-weight and particularly in the fact that small animals have relatively larger brains than large ones. In the preceding chapters, the consequences of this phenomenon for the architectonic structure of the skull and its morphological details dependent thereon have been shown. This knowledge has now to be completed by corresponding references and examples involving the brain-weight and body-weight. The results obtained by Lapicque (Table XXVI), showing the ratio between brain-weight and body-weight in dogs and its dependency on the size of the individual animal, in principle conforms to the ratio between the length of the cranial cavity and the basal length of the skull computed from Wagner's measurements of the various dog races (Table VII), with the difference, of course, that the contrasts between the extreme rates of each side are much sharper in the former case than in the latter.

According to Klatt (1912) there is also a distinct difference in this ratio between large and small wild dogs as may be seen from the following table. As is apparent from a comparison with Lapicque's findings (Table XXVI), the wolf has much more brain sub-

stance in relation to the size of the body than domesticated dogs of the same size (group I), while the fox has less in relation to dogs of the same size (groups VII and XIII); 1 : 270 in wolf against 1 : 355 in dogs, and 1 : 118 in fox against 1 : 88 (78–97) in dogs. According to a later publication by Klatt (1921) the brain-weight of fox with a body-weight of 6000 g amounts to only 50.0 g but that of dogs of the same size to 69.5 g, which is 35 per cent more. Earlier herein it was shown that cats have relatively much larger brains than lions. Dubois (1914) gives the following figures for body-weight and brain-weight; *Felis domestica* 3000 g against 30 g or 1 : 100, but *Felis leo* 135,000 g against 250 g or 1 : 550. According

TABLE XXVIII

Relation between Body-Weight and Brain-Weight in Wild Dogs, After Klatt (1912)

Species	Average Body-Weight in g	Average Brain-Weight in g	Ratio (Body/Brain)
Canis lupus	40,000	147.6	270
Canis aureus	6,836	57.1	120
Canis vulpes	6,120	52.0	118

to the same author (1923) the relative brain-weight of a Shetland pony is almost five times larger than that of a heavy Belgian; while the body-weight of the latter is nine times the body-weight of the pony; its brain-weight is not even twice (cf. Table XXIX). From Hrdlička's (1925) list for primates reproduced in Table XXX, it is most interesting to note that platyrrhine monkeys have relatively much more brain substance than gibbons or the anthropoids, apparently in consequence of their smaller sizes. *Cebus*, in this respect, even exceeds man with a ratio of 17.5 against 46 and 42 of the latter.

TABLE XXIX

Relation Between Body-Weight and Brain-Weight in Horse, After Dubois (1923)

Race	Body-Weight in g	Brain-Weight in g	Ratio
Heavy Belgian	1,040,000	720 (805 cc)	1444
Light Camargue	320,000	525 (585 cc)	609
Shetland pony	128,000	425 (475 cc)	301

From Dubois' ratio of man with 46 for males and 42 for females may be deduced that females have relatively larger brains than males. This would be in accordance with the well known fact that the stature of women generally is about 12 cm smaller than that of man. In Dubois' list of German recruits (given in Table XXVIII), the difference between group I (the tallest) and group IV (the shortest) amounts to 18 cm; the ratio of group I, in correspondence thereto, is 51 and that of group IV 41. Relatively more brain, however, means a relatively larger and more globular-shaped brain case with less developed superstructures and a smaller face. It furthermore implies a tendency towards a later closure of the cranial sutures. That these peculiarities, indeed, constitute the characteristic sex

differences in man may be gathered from all the data given in the literature. According to Rebentisch's (1893) special studies and R. Martin's textbook (1928) the female skull is distinguished from that of the male by the following features: the skeleton of the face is finer and smaller in absolute size, its volume amounting to 30.16 per cent of the cranium in contrast to 32.85 per cent in the male; heavy glabellae and superciliary arches are found in only 17.7 per cent against 69.4 and 80.6, respectively, in the male individual. The frontal air sinuses are smaller. The frontal bone is in erect position (orthometopia) and bulging, while it is flatter and receding in the male. The parietal tuberosity, mastoid process, occipital protuberance and all the tuberosities for muscular attachment are much less developed. For a better distinction of the sexual differences, numerous authors

TABLE XXX

RELATION BETWEEN BODY-WEIGHT AND BRAIN-WEIGHT IN SOME PRIMATES, AFTER HRDLIČKA (1925)

Species	Body-Weight in g	Brain-Weight in g	Ratio
Orang-utang ♂	72,875	371.6	195
Orang-utang ♀	36,439	299.8	121
Siamang ♂	12,744	133	96
Siamang ♀	12,247	134	91
Hylobates agilis ♂	5,946	87.4	68
Hylobates agilis ♀	5,780	79.8	65
Hylobates mulleri ♂	5,516	96.8	57
Hylobates mulleri ♀	6,348	92.6	69
Hamadryas ♂	12,020	142	85
Babuin ♀	22,220	213	104
Various macaques ♂ ♀	2,960	85.7	35
Ateles ♂ ♀	2,089	92.6	23
Alouatta ♂	2,725	44	62
Alouatta ♀	1,170	48.5	24
Cebus ♂ ♀	1,190	69	17.5
Various marmosets ♂ ♀	236	8.4	27

characterize the female skull as having retained its infantile traits, while in the male these have become lost. We shall return to this question later. In addition, the form of the female cranium also differs somewhat from that of the male in being generally shorter and broader and even more brachycephalic in one and the same race. This shortness is not connected with the poorer development of the glabella region, for it is also pronounced when the ophryon is taken at the anterior landmark of the measurement. The degree of differences in cranial indices between male and female and the extent they affect the various races is illustrated in Table XXXI.

The literature contains numerous references to the close correlation between stature and brain-weight in man; the taller the individual, the smaller the relative size of the brain and conversely. This fact is in complete accordance with the general principle disclosed in the preceding pages. Marchand (1902), however, in a special study on the weight of the human brain, denied such a relationship, though he expressly admitted that the existence of a certain dependency of the brain-weight on the stature could not be refuted, especially

TABLE XXXI

SEX DIFFERENCES IN THE LENGTH-BREADTH INDEX OF THE HUMAN SKULL

Race or Source	♂	♀	Author
Hottentot	71.4	74.9	Broca
Australian	68.8	71.4	Krause
Papuan	71.0	73.0	Dorsey
New Caledonian	71.3	74.4	Quatrefages
New Irelander	72.8	76.7	Hauser
Marquesian	75.0	78.2	Broca
Tahitian	75.1	77.4	Quatrefages
Hawaiian	75.5	78.4	Quatrefages
Andaman	80.6	82.7	Pearson
Anglo-Saxon	75.9	76.3	Parsons and Keene (1920)
Medical students, London	78.7	79.5	Parsons and Keene (1920)
Dissecting Room Material, Cambridge	78.01	79.6	Parsons and Keene (1920)
London patients	77.7	79.3	Parsons and Keene (1920)
Danes	80.7	81.5	Sören Hansen (1907/11)
Gipsy	78.3	79.6	Pittard (1905)

in cases of dwarfism where the brain was always relatively rather large. In spite of Marchand's strong denial, it can easily be proved on the basis of that author's own findings, that in normal cases also a certain correlation actually exists. In Table XXXII Marchand's figures relating to stature and brain-weight for males and females have been listed. The individuals are arranged in three groups, according to their size so that we have one group of small individuals, one group of medium-sized and one of tall individuals, for each

TABLE XXXII

STATURE AND BRAIN-WEIGHT OF MAN COMPUTED ON THE BASIS OF MARCHAND'S (1902) FIGURES

Males				Females			
Stature in cm	Average	Brain-Weight in g	Ratio	Stature in cm	Average	Brain-Weight in g	Ratio
139–160	150	1335	8.91	126–150	138	1257	9.10
161–170	165	1405	8.50	151–160	155	1261	8.15
171–192	181	1422	7.86	161–180	171	1302	7.62

of which the average was computed. From the computed ratio of brain-weight and average stature it is evident that the smallest individuals display the highest ratio in males as well as females and the tallest the lowest. This infers that the former have 8.91 g and 9.1 g brain, respectively, on 1 cm stature and the latter 7.86 g and 7.62 g, respectively.

These results conform closely to those obtained by Matiegka (1902) on a different material. According to that author, the relative brain-weight decreases constantly in relation to the increase of the stature as is evident from Table XXXIII.

Since brain-size to a certain extent affects the form of the cranium, as shown above, inasmuch as crania with relatively larger brains have the tendency to become more globular in shape, that is to say, more brachycephalic than crania with relatively smaller brains, one may expect the cranial index to be higher in small individuals than in tall ones. In

TABLE XXXIII

QUANTITY OF BRAIN IN G TO 1 CM STATURE, AFTER MATIEGKA (1902)

Stature in cm	Weight of Brain in g ♂	♀
140–149	—	8.8
150–159	9.0	8.2
160–169	8.6	8.1
170–179	8.3	7.6
180–189	8.1	—

this special case as emphasized by Pittard (1905) only those values are reliable, of course, which have been obtained from studies of a most homogeneous racial material. Pittard's results obtained from measurements of 1200 adult gipsies of one locality (Dobrutscha) are listed in Table XXXIV.

TABLE XXXIV

CRANIAL INDEX OF ADULT GIPSIES AFTER PITTARD (1905)

Males		Females	
Stature in cm	Index (average)	Stature in cm	Index (average)
150–160	78.88	140–152	79.91
160–165	78.69	153–157	79.76
165–170	77.79	158 and more	79.12
170 and more	77.77	—	—
Average	78.28	Average	79.59

All the facts disclosed herein point to the same direction, namely that in recent man also tall individuals have in relation to their body-size smaller brains than short ones and vice versa. Females, who generally are shorter than males, therefore, have also relatively larger brains than males. The characteristic differences in sex between male and female skulls can thus be referred, to a certain extent, to the general difference in body-size. That the cranial sutures close later in females than in males, as ascertained by Frédéric (1906) and other investigators, is in perfect conformity to the other peculiarities of the skull. Unfortunately, I failed to find sufficiently reliable data concerning the proportion between stature or body-weight and cranial capacity or brain-weight in pigmies, on one hand, and giant races like the Shilluk, on the other. We know that the African Efé has an average stature of 140 cm with a cranial index of 79 (Schebesta and Lebzelter), while the average stature of the Shilluk amounts to 182 cm and the cranial index to 73. As to the cranial

capacity, R. Martin (1928) at first states that races of small stature show a relatively larger capacity than those of tall stature and then continues that this relative size of the brain brings about a more globular-shaped cranium like that characteristic of Laps, Andamans and African pigmies. The infantile appearance of the skulls of those races described by various authors depends in general, as does the female skull, upon the relative size of the brain.

Why do small animals have relatively larger brains than large animals? Dubois, Lapicque and Anthony (1928) attempted to find the answer to this question. Their explanation is that the reduction of the body-size cannot be accompanied by a proportional reduction of the brain, for even a small body must rely on a certain quantity of nervous substance, in order to maintain the normal somatic functions of the organs. This quantity cannot be diminished beyond a certain limit. In addition, since the body of small animals has a relatively larger surface than that of the large ones, the supply of nerve fibers must be more abundant. That this is true can be seen from Waszkiewicz's figures quoted by Brandt (1898), concerning a dwarf dog (Bolognese) and a large dog (setter). The number

TABLE XXXV

NUMBER OF FIBERS OF THE SCIATIC NERVE IN DWARF AND LARGE DOGS

Race	Body-Weight in g	Brain-Weight in g	Ratio	Number of Fibers of the Sciatic Nerve	Number of Fibers to 100 g Body-Weight
Bolognese ♀ 12 years old.....	2,695	57.4	40.7	29,675	1,101
Setter ♂ 11 years old.....	20,645	91.2	22.6	50,822	246

of fibers of the sciatic nerve per 100 g body-weight is almost five times more in the small dog than in the large one, while the absolute brain-weight of the former amounts to only 63 per cent of the latter. But according to Dubois (1914) larger brains in proportion to the cortex possess more white matter, that is to say, more nerve fibers than smaller brains. De Vries (1910) reproduced a cross section through the brains of a cat and a puma reduced to the same size, which shows that the brain of the puma has relatively more white matter than that of the cat. De Vries' figures at the same time, however, reveal that the larger brain is more sulcated than the small one. Indeed, this seems to be a general phenomenon. According to Klatt (1921) the fissuration increases with the growing size, dwarf dogs having considerably less fissures than large ones.

Although the real significance of being provided with a relatively large brain is not sufficiently clear, it is definitely known that it does not affect the psychical sphere by increasing the intellectual faculties. Dwarf dogs are known to be less intelligent when compared with setters, pointers or shepherd dogs. Since the greatest contrasts in relative size of the brain are found within this group of domesticated animals, the suggestion lies near at hand to bring it into correlation with the domestication itself. But even an approach from this angle does not lead very far. Darwin (1892) was first to call attention to the

fact that domestication had the tendency to decrease the weight of the brain; the brain of the domesticated rabbit, according to that author, is 11–54 per cent lighter than that of the wild rabbit. Lapicque (1907) confirmed Darwin's observations; he found the decrease of the brain-weight to amount to 15 per cent in rabbits, and the same should be true for cattle and ducks. In respect to dogs Klatt (1912, 1921) is inclined to accept the view that domestication leads to diminution of the brain-size but his figures show that such only applies to the large group of dog when compared with the wolf. In this case the cranial capacity of dog is 15.6 per cent smaller than the capacity of a wolf of about the same size. When, however, a small wild dog like the fox is compared with a domesticated dog belonging to a race of the same body-size, it becomes apparent that the brain-weight of the fox is approximately 35 per cent smaller than that of the dog. In Table XXVIII the body-weight of the fox is listed as 6120 g and the brain-weight as 52 g, while the brain of a dog of the same size (groups VII–VIII of Table XXVI) weighs about 68 g or 16 g more. In spite of Klatt's positive results, Dubois (1922) criticizes Leche (1922) who compared the cranium of a dwarf pinscher with that of a fennec and found the former larger than the latter.

The fundamental idea underlying all these discussions is the belief that the size of the brain is in some way directly connected with the mental faculties. A decrease of the size in consequence of domestication would thus be tantamount to an impairment of the natural instincts, etc. As already stated above, Dubois considers the cephalization-coefficient a type of measure of the psychical factor. But as pointed out already by von Bonin (1937), all these attempts to analyze the relation between body-weight and brain-weight suffer from three deficits: (1) they presuppose a correlation between intelligence and brain-weight, (2) they make suppositions about the intelligence of animals which are unproved and (3) they are based on a conception of cortical functions which can no longer be considered valid. How far Dubois ventured in this respect may be judged from his explanations of special cases of enlarged brain. Canidae should owe their high cephalization to the better developed sense of smell and hearing, the elephant to its trunk "with specific energies," American monkeys, exceeding even the anthropoids, to the prehensile tail, and man, to his hand. As has been shown above, dogs certainly do not have a better sense of smell than foxes of the same size, though they have 15 per cent more brain than the latter. Klüver (1933, 1937) and Warden (1940) found that monkeys belonging to the genus *Cebus* are equal to anthropoids in their ability of utilizing objects as tools. But *Cebus* is not equipped with a genuine prehensile tail and has the same cephalization-coefficient as *Ateles*. That the development of the hand and nothing more should be the underlying cause of the extraordinary enlargement of the human brain, as Dubois suggests, is entirely out of the question. With much more justification can the claim be made that, on the contrary, the enlargement of the brain constitutes the cause underlying the special accomplishment of the hand.

With this discussion we already broached the subject concerning the difference between relative and absolute size of the brain. Dwarf dogs have relatively more brain substance than large dogs but anthropoids have absolutely more brain than dogs, and man still more than anthropoids. It has been demonstrated that the characteristic stages undergone by the human skull in the course of the phylogenetic evolution corresponds not only in principle but also in details entirely to those extreme forms in the dog series: the primary anthropoid-like type to large dogs and the last phase, recent man, to dwarf dogs. But

recent man is not a dwarf when compared with his simian ancestor. His having a larger brain, therefore, is not a consequence of dwarfism but one of an absolute increase in size during evolution. The effect on the skull which lodges the enlarging brain is the same as in those cases in which the brain is only relatively more spacious. For the alteration of the skull form is only a question of space. In 1923 Dubois advanced the seductive theory that a relative increase of the nervous system should be the effect of an ontogenetic process, and an absolute increase the result of a phylogenetic one. In the first case, the enlargement should be due to an increase in volume of the nerve cells, while in the latter to an increase of the number of cells by means of cell division, in other words, relatively large brains should have larger cells, absolutely large brains, however, more cells. Yet Dubois' attempt to prove this assumption by referring to figures taken from other workers is not very convincing. Referring to Brodmann he noted, for instance, that the maximum size of the nerve cells of the lion amounts to 69.5 μ and that of the cat to 69.0 μ. This is practically no difference, however, although one may expect—provided the theory is correct —the cells of the cat to be much larger than those of the lion since the ratio of the brain-weight and body-weight totals 106 in the cat against 546 in the lion. A satisfactory explanation thus remains to be found. As far as I can see, the condition is as follows. Size or weight of the brain, that is to say, the space occupied by the brain is directly decisive for the size of the cranium and, on account of the known correlation between cranium and face, also for the proportion and topographical interconnection between these two constituents. But increase in brain-size or brain-weight in phylogenetic evolution constitutes only one phase of the problem. Not less important is the increase in the cortical substance, the seat of the psychical process. The increase of the cortical substance is effected by a continuous enlargement of the surface. For this purpose it is not necessary to enlarge the brain itself and thereby to expand the space required for its lodging but it can better be achieved by folding in the surface. In the phylogenetic development of the brain, that is, if it is absolutely enlarged, the increase in size must go hand-in-hand with the fissuration. In cases, however, where the brain is only relatively enlarged as in dwarfs, the relative increase in size may be balanced by a loss of fissuration, with the psychical level remaining unchanged. The loss by the diminution of fissuration may even exceed the gain in size. As already mentioned above, Klatt (1921) showed that dwarf dogs have less fissuration than large dogs, and the same conditions are evident in de Vries' (1910) illustrations representing cross sections through the cerebrum of cat and puma. Unfortunately, no exhaustive investigations are available in respect to quantities and qualities of the cortex of small and large animals. If we examine the conditions and determinant factors of dwarfism itself, the answer is not more satisfactory. On the title-page of his book on the psychical basis of personality (1931) Stockard gives the photographs of six heads, among them the heads of an English bulldog, a Pekingese, a human dwarf and a man of normal size with a face like a bulldog. The explanation given reads: "These types are often hereditary but in all cases are associated with peculiar reactions of the glands of internal secretion." In the text as also in earlier special treatise (1923) Stockard fails to outline these peculiar reactions. He speaks, with special reference to certain dog breeds (apparently bulldogs and dwarf types), of achondroplasia and structural distortions connected with strange and widely modified complexes of the endocrine glands. In consequence of that conception, he considers large types like the Great Dane, the Irish staghound or St. Bernard as typical

examples of acromegaly and dwarf types as an indication that the thyroid gland does not function "normally." Yet these statements are somewhat disappointing for they do not go beyond generalities, nor are they supported by precise data which could serve as proofs. Unfortunately, Keith (1922) was just as brief in his often cited publication in which he discussed the evolution of the human races in the light of the hormone theory. Keith regarded the super-structures of the gorilla skull as an indication of acromegaly, that is to say, as "an example of the pituitary mechanism at work in the evolution of types." But, strangely enough, the same mechanism is also made responsible by the author for the shaping of the European type of the human races. The orang is regarded as the bulldog amongst anthropoid apes and "bulldogism" as achondroplasia and, therefore, as the expression of "disordered thyroids." Dwarfism, generally, should be the result of the tendency for the thyroid mechanism to become dominant. These statements also are devoid of any substantial evidence of the pituitary body or the thyroid gland differing in these special cases in structure or function from the "normal" organs. The super-structures of the gorilla skull which, of course, are homologous to super-structures of all large animals with a relatively small brain, cannot be interpreted merely as the effect of acromegalic conditions but must be considered as the result of a characteristic disproportion between the size of the cranium and face or brain-weight and body-weight (cf. chapters II and III). The contrast in the appearance of the skulls of gorilla and man in the first place depends upon the differences in growth rates. As will be shown subsequently, these relations may be regulated by hormones but, so far, everything published on that subject failed to go beyond general speculations.

VI. Fetalization Theory and Relative Growth

Studer (1901), following Rütimeyer, already interpreted the peculiarities of the skull of small dogs as being due to the retention of juvenile characters. In extreme dwarfs even fetal features should be preserved. Schmitt (1903), in a special study on the development of the dog skull, was able to demonstrate that skulls of newborn puppies of large dogs, like the St. Bernard, for instance, or the Newfoundland, do not differ essentially from those of dwarf dogs, like the black-and-tan terrier; but while the former change the original form rapidly in the course of postnatal development, the latter retain it practically unchanged up to the most advanced age. Schmitt illustrates the growth of a St. Bernard skull by placing side-by-side the skull contours of a newborn, a four weeks old, and a ten weeks old puppy. These are reproduced in Fig. 45 here (*A*, *B*, *C*) with the anterior limits of the cranial cavity indicated by a dotted line. It is of special interest to note the extension of the frontal bone participating in the formation of the brain case in the newborn and the alteration of the position in the course of further development. In the newborn stage the frontal bone forms the entire anterior part of the brain case, the latter, or more correctly the cranial cavity, extends forward up to the nasion (*A*). The more elongated the skull becomes by pushing the face forward, the more the brain case itself will fall back, so that after ten weeks (*C*) only the posterior portion of the frontal bone participates in that formation, while its major portion now serves to construct the face, that is to say, the postorbital process with the enclosed air sinus. The extraordinary elongation of the face is best illustrated by comparing the position of the anterior boundary of the cranial cavity in the newborn (*A*) with that of the ten weeks old puppy (*C*). In the first case,

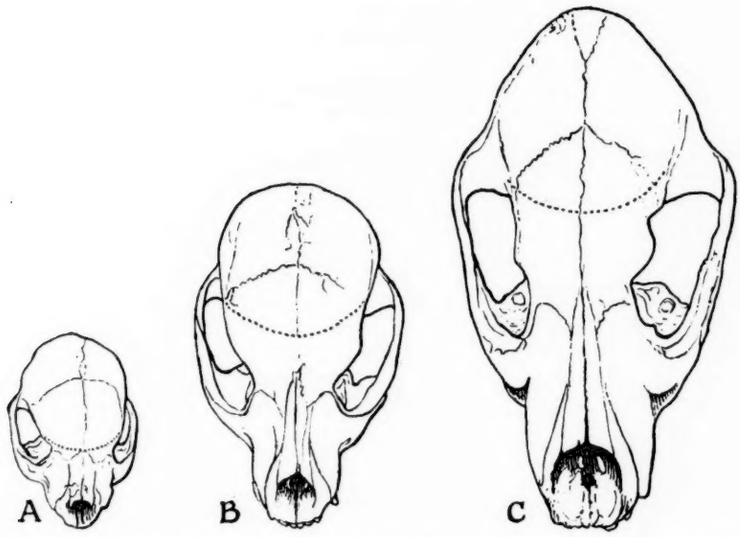

FIG. 45. Post-natal growth of the skull of a St. Bernard after F. Schmitt (1903). 5/6.
A. Newborn female. *B*. Male four weeks old. *C*. Female ten weeks old.

this boundary lies on the same vertical plane as the anterior site of junction of the zygomatic arch but in the second on the posterior one. The elongation of the face and the corresponding development of super-structures can also be made evident by comparing median sections through the skulls of newborn and adult individuals of the large type. Fig. 46

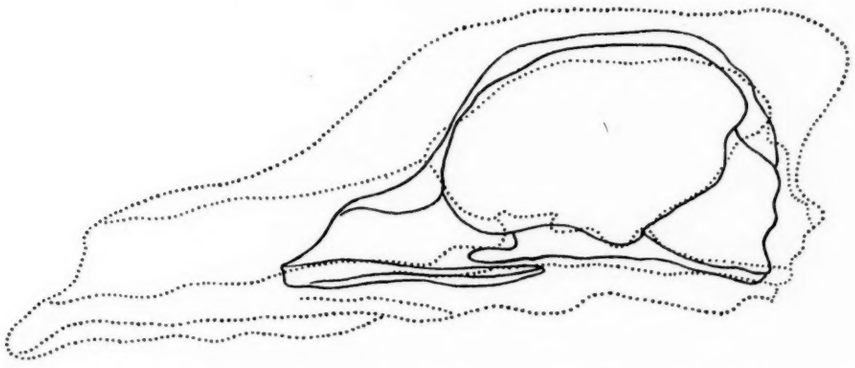

FIG. 46. Diagrams of median sections through the skulls of an adult Newfoundland (· · · ·) and a newborn wolfhound (——) superposed and reduced to the same size of cranial cavities.

shows sections of a newborn wolfhound and an adult Newfoundland with the cranial cavities superposed and reduced to the same size. The outlines of the larger skull distinctly show the proportions of the elongation of the face and the height and bulkiness of the superstructures. To what degree, on the other hand, the skull of a dwarf type retains the fetal conditions is illustrated by Fig. 47. Herein the outlines of the median section through the skull of the same newborn wolfhound used in Fig. 46 are superposed on that of an adult

dwarf pinscher with the cranial cavities reduced to corresponding size. There really is no difference in the proportions of the entire skull and the relations of brain case and face between newborn wolfhound and the adult dwarf pinscher.

The same parallelism as exists between the skulls of adult dwarf types of dogs and recent man, on one hand, and adult large types of dogs and anthropoids or prehominids, on the other, can also be found in regard to fetal and juvenile stages. It is a well known and frequently emphasized fact that fetal and juvenile skulls of anthropoids bear a closer resemblance to the human form than such of adult stages. In Fig. 48 a fetus of a gorilla (*A*) is compared with a Negro fetus (*B*) of the same stage of development. Both show the original position within the uterus. The forehead of the gorilla is as high and bulging

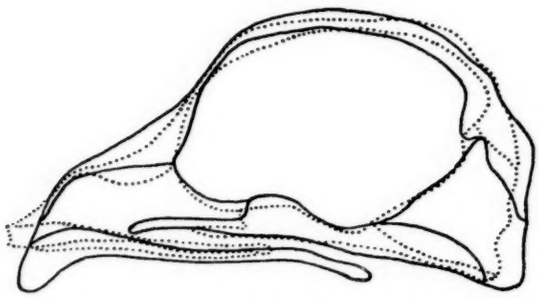

FIG. 47. Diagrams of median sections through the skulls of an adult dwarf pinscher (——) and a newborn wolfhound (· · · ·) superposed and reduced to the same size of cranial cavities.

as in the Negro. Of course, there is a strong prognathism in the former but when considered as a whole, the differences are by far not as pronounced as in the adult gorilla; the appearance of both cranium and face is rather human-like. Kollmann (1905) was first to utilize these facts in advancing a special theory of human evolution. He assumed that the first hominids had highly vaulted skulls like the ape fetuses, and since smaller types generally should precede large ones in phylogenetic evolution, man should have been evolved from pigmy forms resembling juvenile apes. But it was left to Bolk to draw far-reaching conclusions from the similarities of fetal and juvenile stages. In the last publication on this problem (1926) he condensed the essence of his viewpoint to the sentence: man represents a fetus of a primate which has become mature. Bolk distinguishes primary and consecutive characters. Primary characters are such as have been developed directly by the effect of factors responsible for the production of the human form; consecutive characters, however, are mere adaptations to the erect posture. The former group should include the following human peculiarities: orthognathism, hairlessness, loss of pigmentation, Mongolian fold, central position of the foramen magnum, large brain volume, persistence of the cranial sutures, construction of hand and foot, etc. These characters, according to Bolk, are transitory conditions specific to all primates but have become fixed in man as permanent characters, while in apes they become lost in consequence of the continuing differentiation. The ape fetus shows a more human aspect not because the apes are descendants of a more human-like ancestor as a consequent application of Haeckel's biogenetic law would suggest, but because man preserves the fetal type until the end of his growth. In earlier publications, Bolk defined the human manner of development as "conservative" and that of the

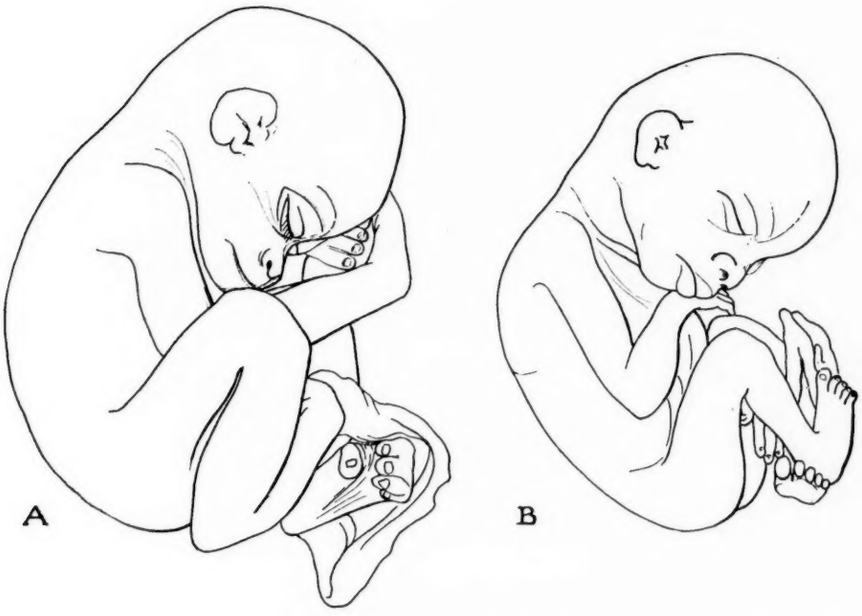

FIG. 48. Fetus of gorilla and man of the same stage of development. *A*. Gorilla, Coll. Senckenberg Museum in Frankfort a/M. *B*. Modern man (negro), after H. Friedenthal (1914).

apes as "propulsive" and from this difference, considered fundamental, he infers that man has no close connection with the anthropoids.

Bolk's way of explaining the essential differences between human and simian evolution partly met with approval and partly was rejected. The fact that juvenile monkeys or apes show a relatively more erect and bulging forehead and thereby bear a closer resemblance to man than adult stages do, also underlies Schindewolf's (1936) attempt to prove that the development of each new type in phylogenetic evolution takes its origin in early ontogenetic stages but at no time in adults. The more progressed and higher organized the new type appears and the more it, therefore, differs from the preceding phase, the earlier its formation in fetal life has to set in. In regard to the development of the skull, there is, according to Schindewolf, a decisive difference between anthropoids and all genuine apes, on one hand, and the prosimians and all lower animals, on the other. At no time, neither in juvenile nor in adult stages of the latter category, should the cranium dominate over the face as is true in the human skull. Consequently, an ontogenetic reversion of these conditions appears to be impossible.

Before entering into a discussion of these theories, it must be pointed out that the presupposition on which they are based is only partly correct. It is, of course, true that fetal or juvenile stages of anthropoids and all other apes or monkeys display a more human-like appearance with regard to the development of forehead and face. The reason for this peculiarity is obvious, for it is exactly the same as the reason why the skull of pigmy chimpanzee resembles man closer, regardless of its stage of development (cf. chapter II), than the skull of a chimpanzee of normal size does. In all fetal and juvenile stages the size of the brain is relatively much larger than in adults. This predominance of the brain, how-

ever, is not in the least confined to the higher primates as suggested by Schindewolf in particular but is characteristic of not only all mammals but also of all vertebrates. Figs. 45–47 demonstrate that newborn dogs of large types have, in contrast to the adults, a marked bulging forehead with the cranial cavity and the brain extending forwards (and downwards) to the nasion. In adult dwarf dogs these fetal conditions are "stabilized" as may be noted in Figs. 1–5 and 47. Since Schindewolf refers in particular to the prosimians as an example in which the cranium does not dominate over the face even in juvenile stages, Fig. 49 illustrates the skulls of a fetal (*A*) and an adult (*B*) specimen of *Lemur catta* (after F. Wood-Jones, 1929). Even a hasty examination will reveal that the prosimians also do not constitute an exception to the general rule that small skulls lodge relatively large brains and large skulls small ones.

It is a well known fact that in ontogenetic development the nervous system is first to be differentiated and that its rate of growth exceeds that of all other organs. As long as this rate remains unchanged, the brain determines the proportions of the two main

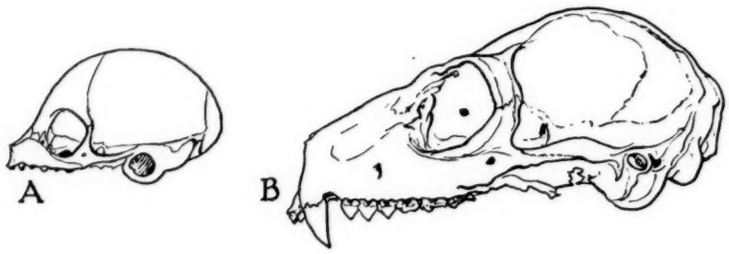

FIG. 49. Skulls of *Lemur catta*. 3/4. *A*. Fetal specimen after F. Wood-Jones (1929). *B*. Adult male specimen, Coll. A.M.N.H. no. 100596.

constituents of the skull, brain case and face, the former predominating, the latter restricted. Subsequently during the development the moment will arrive when the growth of the central nervous system becomes diminished or ceases entirely. Then the hitherto restricted organs become "propulsive" and the proportions reverse. This is what occurs in great apes at a certain period of their postnatal life, approximately at the time when the deciduous dentition is fully erupted. In man, however, the growth rate which in general is already considerably higher than in anthropoids, remains unchanged, or its reduction covers a longer period and thereby exerts an arresting influence on the face as long as the growth is active. This is apparently what Bolk had in mind when speaking of the "conservative" character of human evolution. That it, nevertheless, is quite different in nature from Bolk's conception will be shown below.

When we take the relation between brain-weight and body-weight as a basis again, it is easy to ascertain the gradual decrease in the predominance of the former during ontogenetic evolution and the time of fixation of the definitive state. Table XXXVI contains all the reliable data found in Ziehen's (1899), Marchand's (1902), Handmann's (1906) and R. Martin's (1928) publications. While the ratio between brain-weight and body-weight amounts to 1:4 in the fourth month, it increases to about 1:9 at the time of birth, to about 1:15 at the time of the full eruption of the deciduous dentition and to over 1:40 in the adult.

In anthropoids as in all other mammals, the general conditions are the same; in fetal life or early youth the percentage of brain-weight to body-weight is, in correspondence to the age, much higher than in later and adult stages. But, of course, it results in a considerable difference in the degree of the ratio when small or large-sized animals, irrelevant of the group they belong to, are compared inasmuch as the brain of the former is relatively always larger than that of the latter. Unfortunately, exact records of anthropoid ages are not available which could be considered as equivalents to those of man. The only reference I was able to find in the literature is contained in Max Weber's record that the brain-weight of a juvenile female *Symphalangus syndactylus* with complete milk dentition amounts to 116 g and the body-weight to 2057 g, the ratio thus to 18. According to

TABLE XXXVI

Change of Ratio between Brain-Weight and Body-Weight During the Ontogenetic Evolution of Man

Age	Stature in mm	Brain-Weight in g	Body-Weight in g	Ratio of Body-Weight to Brain-Weight	Author
4th fetal month	—	29	120	4.1	Daffner and Ziehen (1899)
5th fetal month	—	44	205	4.7	
7th fetal month	—	141	1010	7.2	
Newborn ♂	506	357	3.451	9.4	Handmann
Newborn ♀	501	354	3.219	9.0	
Up to 1 month ♂	511	371	3.312	8.9	Marchand, R. Martin
Up to 1 month ♀	506	361	3.209	8.9	
5–6 years old ♂	1079	1215	17.950	14.8	Handmann
5–6 years old ♀	1079	1194	17.570	14.7	
Adult ♂	1650	1375	63.010	46.0	Dubois
Adult ♀	1550	1285	52.170	42.0	

Hrdlička (1925), the corresponding figures of an adult female Siamang are 134 and 12247 g with a ratio of 91.5. The definite ratio in this case is 118 per cent higher than in man, while at the time of the completion of the first dentition the difference totals only 18.3 per cent. Since the cranial capacity of an adult Siamang and that of a juvenile with complete milk dentition is practically the same (average 125 cc in both cases) the rapid increase of the ratio after this phase indicates that the body, including the masticatory apparatus, grows at a much faster rate than in man while the cranium (brain) remains stationary.

That man had a larger head from the beginning of the ontogenetic development than orang-utang and gibbon can be inferred from Schultz's (1926 c) figures in Table XXXVII. It is interesting that this predominance diminishes gradually so that finally it is more than balanced. That means that adult orang and gibbon have relatively larger heads than man.

Bolk considers the human form a morphological equivalent to a primate fetus which has become mature or, in other words, a neotenic primate type. According to De Beer's (1930) definition of paedomorphosis or neoteny, this phenomenon would imply that "young features of the ancestor have been retained in the adult stage of the descendant." This

TABLE XXXVII

INDEX OF GROWTH CHANGES IN RELATIVE HEAD SIZE (AVERAGE HEAD-DIAMETER IN PERCENTAGE OF ANTERIOR TRUNK HEIGHT), AFTER ADOLPH H. SCHULTZ (1926 c)

Genus	Prenatal 4th–5th Month	At the Time of Birth	Adult
Man	78.0	59.0	31.0
Orang-utang	65.0	60.7	31.8
Gibbon	63.75	60.85	31.75
Cebus	63.2	70.9 (6th–8th)	30.9

infers a relative retardation in the developmental rate of the body compared with the reproductive glands, that is to say, maturity is reached before other organs have completed their development. If man is to represent a neotenic primate type, we should have to expect him to mature at an earlier time than the anthropoids, especially if the brain-growth, to the size of which Bolk refers, is taken as basis for comparison. But, strangely enough, Bolk himself claims that the maturity in man is retarded and not accelerated when compared with the conditions of anthropoids. Apart from this discordancy, there is really no decisive difference in time-limit at which maturity sets in in man and anthropoids. In both cases, maturity is reached before the second dentition is completed. Girls of races living under tropical conditions begin menstruating already at the age of ten. As far as we know, the time of the onset is only slightly earlier in the great apes (between eight and ten years). With regard to the cessation in brain-growth, it coincides in both cases with the eruption of the third molar. According to Zuckerman (1928) the third molar in the chimpanzee does not erupt before 15, probably later.

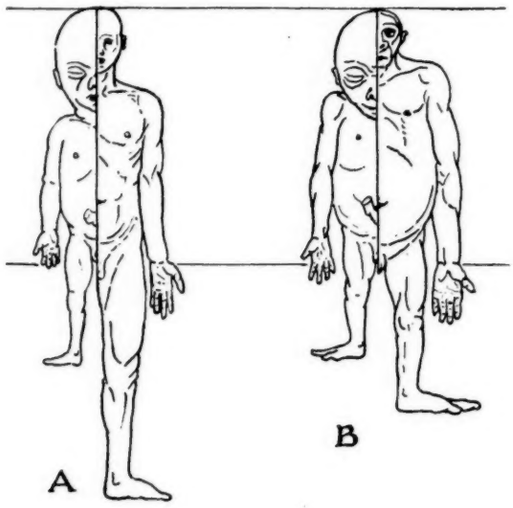

FIG. 50. Diagrammatic representation of the exact body proportions of fetal (left half) and adult (right half) stages of man (*A*) and gorilla (*B*). Reduced to the same sitting height. After Adolph H. Schultz (1926 a).

But even disregarding all these facts, man is neither "conservative" nor less "propulsive" than the anthropoids, as suggested by Bolk. Fig. 50, taken over from A. H. Schultz (1926 a), illustrates to what extent the proportions of the human body (*A*) and those of the gorilla (*B*) have been subjected to alterations during the post-fetal growth. In both cases, the height of trunk plus head serves as a basis. It is evident that the fetal proportions have been abandoned both in man and in gorilla. The head is considerably reduced in relative size, while the trunk and limbs have become increased. This increase is particularly pronounced in the lower extremity. The length of the leg amounts to 158 per cent of the length of the trunk in man against 113 per cent in gorilla and chimpanzee. But in the human newborn the length of the leg totals only 40 per cent of the entire length

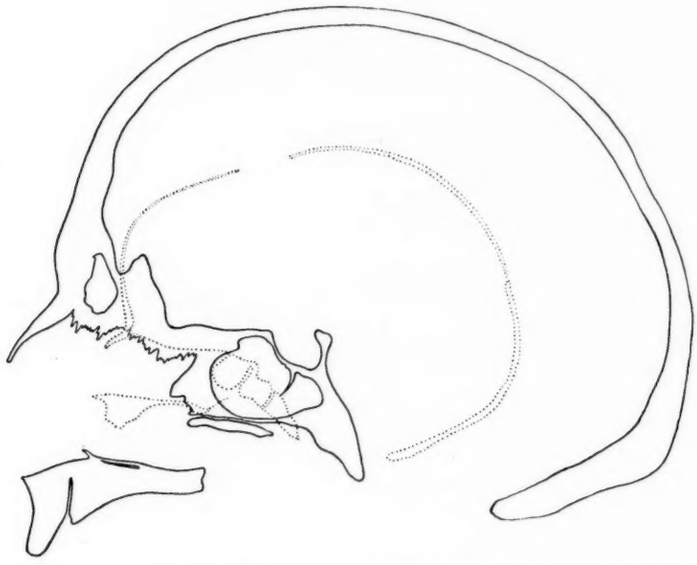

FIG. 51. Median sections through the skulls of a newborn male child (· · · ·) and an adult male European (——) superposed on the basal line. After H. Welcker (1862). 1/2.

of the body, while in adult man it is 52 per cent. Considered as a whole, man deviates from the fetal conditions much more than the gorilla does. It should thus seem more justifiable to consider gorilla the "conservative" type.

The essential difference which characterizes the ontogenetic development of man, on one hand, and anthropoids, on the other, is not the retention of fetal features in the first case and their abandonment in the latter but the preservation of the fetal growth proportions for a longer period in man and their early reversal in the great apes. In man as also in anthropoids, there primarily exists in ontogenetic evolution an allometry between cranium (brain) and face in that the growth of the cranium prevails and that of the face lags behind (positive allometry). Later the conditions change. While in man the growth proportions remain almost the same until the end of the growth, in anthropoids the brain lags behind and the growth of the face becomes dominant (negative allometry). "Conservative" means the preservation of the fetal growth rate but not the preservation of fetal features. Fetal features to which Bolk refers as, for instance, orthognathism, central

position of the foramen magnum, persistence of the cranial sutures are conditioned by a relatively large brain and brain case and persist in their original character during the postnatal life only because brain and brain case retain their predominance in growth or, in other words, they remain positive allometric; however, they are of transitory nature in the great apes because their prevalence becomes lost or, in other words, brain and brain case change to negative allometry.

The characteristic difference in man and anthropoids can best be illustrated by median sections through the skulls of a newborn and an adult of each superposed on the nasion-basion-line. Fig. 51 copied from a drawing by H. Welcker (1862) shows the human conditions. The skull of the adult appears as an equal enlargement of that of the newborn with brain case and face increased by retaining the same proportion. Fig. 52 taken from the

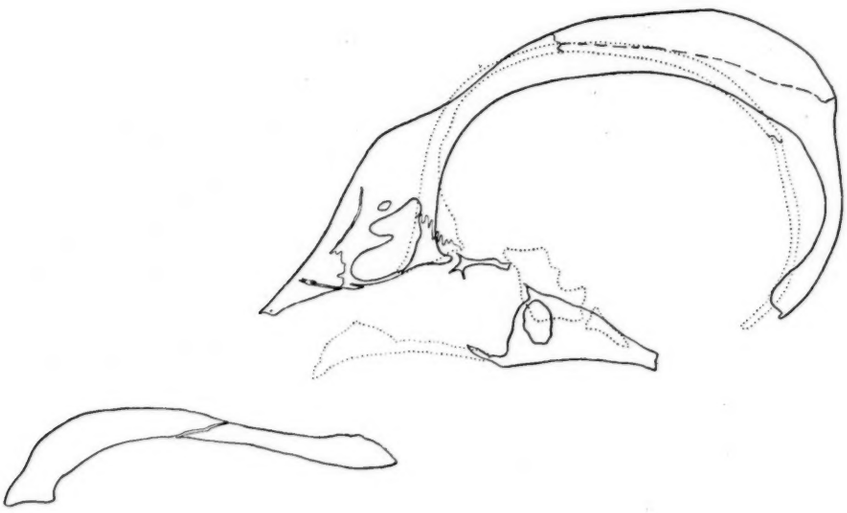

FIG. 52. Median sections through the skulls of a juvenile orang-utang (· · · ·) and an adult individual (——) superposed on the basal line. After H. Welcker (1862). 1/2.

same source displays the conditions of an orang-utang. The skull in this case is not that of a newborn but that of a rather young individual. In contrast to man, a very striking disproportion exists between juvenile and adult stage. While the outlines of both cranial cavities are fairly congruent indicating that no further enlargement of the juvenile skull has taken place, the face, that is, the upper jaw extends forwards and downwards to a considerable degree.

That which holds good in regard to the relation between man and great apes is also valid for dwarf and large dogs. As Schmitt (1903) proved and as Figs. 45–47 illustrate (see above) the skull of an adult dwarf dog resembles completely in form and proportions the skull of a newborn, while the adult skull of a large dog differs considerably in form as well as in proportions. To speak of a retention of fetal features in this case like Studer (1902) and Schmitt (1903) did confuses the real conditions as much as was true of man. Klatt (1913) already objected to consider the skull of a dwarf dog as merely a fetal form arrested in its development; morphologically and physiologically it represents the skull of an adult animal. "That dwarf and juvenile forms show a similarity in appearance cannot

be explained by dwelling upon the juvenile phase. But the same smallness in size in both cases maintains certain functions at approximately the same level." As shown in chapter II, the teeth also display dwarfish characteristics in size, form and pattern; these alterations, however, do not concern the juvenile set of teeth but the permanent teeth. Dwarf dogs differ in their growth proportions from the large dogs to the same extent as man from anthropoids. In dwarf dogs the fetal conditions of the growth relation between brain (brain case) and face persist, while in large dogs this relation becomes reversed with the definitive arrest of the brain growth.

It is certainly in close connection with the nature of dwarfism that the growth itself is not retarded but rather accelerated in dwarfs when compared with large dogs. That

TABLE XXXVIII

RATE OF INCREASE IN LENGTH OF THE SKULLS OF A ST. BERNARD AND A BLACK-AND-TAN TERRIER CALCULATED ON THE BASIS OF SCHMITT'S (1903) MEASUREMENTS

Race	Measurements of the Skull	Newborn	5–6 Months	Adult	Percentage of the Definitive Length Attained	
					At Birth	At 5–6 Months
St. Bernard	Basal length	55	178	219	22.8	81.3
	Length of the cranial cavity	44	106	130	33.9	81.5
	Length of the palate	35	103	123	28.7	83.8
	Average	—	—	—	28.5	82.3
Black-and-tan terrier	Basal length	27	79	88	30.7	89.7
	Length of the cranial cavity	24	59	66	36.4	89.5
	Length of the palate	17	40	48	35.5	83.3
	Average	—	—	—	34.2	87.5

this is the case may be computed on the basis of the data supplied by Schmitt (1903) including certain length measurements of the skulls of a St. Bernard and a black-and-tan terrier. The results obtained are listed in Table XXXVIII. At the time of birth the skull of a dwarf has already attained 34 per cent of its definite length and at the age of 5–6 months 87.5 per cent, the large dog, however, only 28.5 and 82.3 per cent, respectively, at the same time.

The cause underlying dwarfism is unknown. Dwarfism can be due to scantiness of the formative substance; it can also be the effect of a disturbance in thyroid secretion. But whatever the reason may be, the particular form of the skull and the specific proportions between brain case and face are dependent upon the body size. In dogs dwarfism occurs as a variation within the same species; the same is true of dwarfism in chimpanzee. Within the group of Felidae in which the small wild and domesticated cats represent dwarfs and the lion and tiger the large types, dwarfism occurs within the same family. The discrimi-

nation between species in one case and family in the other is permitted, however, only if we strictly hold to the established zoological classification.

In man and anthropoids the transformation of the skull follows the same law of relative growth which determines the relation between brain and body. But when compared with its application to dwarfism two important differences become apparent. First, the transformation of the human skull appears as a process of phylogenetic evolution and not as a mere variation among living representatives of the same species. Second, man is not a dwarf when compared with anthropoids. The existence and the appearance of the prehominids *Pithecanthropus* and *Sinanthropus* prove that his immediate ancestor was of the same body-size but his brain volume was less. This fact forces the conclusion that the brain had increased during phylogenetic evolution while the body retained its original size. The enlargement of the brain is, therefore, an absolute and not a relative one. Since the effect of such an enlargement on the structural particularities of the skull remains the same, regardless of the special incentive, the brain must be considered to be the true factor which determined the characteristic transformation of the human skull.

VII. Analysis of Morphological Characters and Human Evolution

Bolk (1926) in his fetalization theory divided, as was pointed out above, the morphological human characters into two groups, primary and consecutive ones. The first are considered primarily responsible for the specific human form, the second only as adaptations to the erect posture. Bolk's classification as well as his interpretations are not consistent nor convincing. The decrease in pelage and pigmentation and the construction of the foot, for instance, should belong to the first category, whereas in reality the specific structure of the human foot is an excellent example of adaptation to the erect posture. On the other hand, decrease in pigmentation is not at all a primary human character, for negroes certainly do not show less pigment in skin, hair and eyes than apes. But the significance of Bolk's attempt lies more in the fact of having recognized the inequality of morphological characters. Klatt (1913) arrived at such a conception much earlier. The great morphological differences of the skull so apparent in dogs of different size led him to the conclusion that extrinsic differences alone were unsuitable for differentiating races but that the intrinsic causes which determine the special characters should first be ascertained or, in other words, the characters should be evaluated according to their real nature. Klatt did not attempt to undertake such a classification himself. What the author had in mind, of course, is a precise analysis of correlations on a purely morphological basis.

We know there is still one other way of analyzing morphological characters, a course taken by geneticists. The genetical point of view lays but little stress on the special external appearance of a given morphological character and instead considers it more or less exclusively a product of concurrence between an intrinsic hereditary disposition of the organisms represented by a specific factor and environmental conditions. This disposition is bound to a special gene contained in the chromosomes. Correlations can also be found in these cases but such "genetical correlations" are due to the factors being located either in one and the same gene or in one and the same chromosome. The frequency in occurrence of those genes which may produce changes in more than one character, however, is not well known, according to Dobzhansky (1937). A good example of such manifold or pleiotropic effects of a single gene is supplied by Timoféeff-Ressovski as cited by Rensch (1939). The

gene "polyphaen" induces the following peculiarities in *Drosophila funebris:* irregular distribution and arrangement of the bristles of the eye facets, abnormal pigmentation of the abdominal segments, often also a thickening of the posterior margins of the tergits, distended wing-spread, multiple interruption of the wing nervures and reduction of the bristles of head and thorax. This confusion proves that there is no structural connection between the single effects of such a gene. If, however, relative smallness or relative largeness of the brain infers a special appearance of the skull, each characterized by different morphological peculiarities, then a close morphological correlation exists between brain-size and, for example, the formation or non-formation of supra-orbitals. But if albinotic cats are deaf or human individuals with extensive hypertrichosis of the face at the same time show defective dentition, the coincidence is due to those "genetical correlations" while a morphological and functional linkage between the two phenomena cannot be demonstrated.

When the morphological characters of the skull of a Pekingese, on one hand, and those of an Irish wolfhound, on the other, are analyzed, it becomes evident that their real fundamental character fails to reveal any alteration, in spite of the great differences in the general form as well as in important details. The roominess of the brain case in dwarf dogs does not influence, for example, the position of the foramen magnum or the evenness of the base. The foramen shows no tendency to tilt downwards nor does the base show a deflection as is characteristic of man in contrast to the apes (cf. Figs. 3, *A*, 47 and 34, *A–C*). These characters specific of the species dog are fundamental characters or those of the first order. They are common to all variations independent of the size of the body or the size of the brain. But apart from these characters there are those which are specific of the variation and dependent upon other factors. These in large dogs comprise small brain case, heavy supra-orbitals, large frontal air sinuses, high crests, far projecting face, large and well developed teeth and, on the other hand, the opposing characters: large brain case, small or no super-structures and frontal air sinuses, reduced face, small and rudimentary teeth in dwarf dogs. These characters may be called special characters or those of the second order. But we still have a third category which may be demonstrated in the case of Felidae. It has been shown that specific morphological differences in the skulls of wild or domesticated cat and those of lion are of the same nature in principle as those between small and large dogs, that is to say, they are dependent upon the relative size of the brain when compared with the size of the body. Thus, in the case of Felidae we also have two categories: characters of the first order—such as are typical characters of the Felidae family—and characters of the second order which determine the small Felidae type (cats in the strict sense of the word) or the large one (lion or tiger). It is a well known fact that the skulls (and the skeleton) of lion and tiger are identical in form and details. There are some peculiarities, however, which, according to certain authors, should make it possible to distinguish the two types from each other, as for instance the course of the naso-frontal suture, the formation of the base of the mandible and the configuration of the inner lobe of the upper carnassial. But Pocock (1935) who examined all the supposed differences on a large number of specimens arrived at the conclusion that "most of these differences break down under the examination of far more skulls than were available to those who put forward the claim." The differences, according to that author, are average rather than absolute, all of them being subject to individual or racial variation. There

really is no decisive divergence between lion and tiger when stripped of their hides. The character of the hide or more precisely the texture and color of the hair and the color pattern, therefore, determines whether the large cat type is a lion or a tiger. One could exchange the hides of lion and tiger without implicating the fundamental and special cat characters. What is true of the Felidae also applies to dogs. Whether dwarf and large dogs have long and curved or short and straight hair, long and hanging or short and standing ears, a stretched or curved tail has no bearing on either the fundamental or the special characters which are only determined by the individual belonging first to the Canidae family and then, within this group, to a certain order of size. All the enumerated characters are of secondary importance and may be ranged within the third order. The antlers of the deer family also belong to this order. It is easy to verify that all features we may find in any type of mammals or vertebrates can be ranged within one of these categories.

The morphological characters defining a given type can thus be grouped into three classes which I tentatively designate as fundamental, special and secondary or characters of the first, second and third order. The fundamental characters are apparently identical with those which determine the family and all categories superior thereto. Special characters may in some cases determine the genus, in others the species and again in others only the race, while secondary characters correspond only to species, subspecies or racial characters. Special and secondary characters are not restricted to only one of these categories because of the impossibility of demarcating them sharply if we should follow the usual rule of classification. This would become still more difficult if the modern tendency to disregard all morphological characters when defining species, subspecies and races meets with general acceptance. Mayr (1940), for instance, defines the species as follows: "A species consists of a group of populations which replace each other geographically or ecologically and of which the neighboring ones intergrade or hybridize wherever they are in contact or which are potentially capable of doing so (with one or more of the population) in those cases where contact is prevented by geographical or ecological barriers." In domesticated dogs dwarf and large types and their various differentiations are generally ranged within one and the same species and only distinguished as representing different races, in spite of the fact that the morphological differences are not less than those existing among certain members of other families but then attributed to different species. Lion and tiger, for instance, do not differ more than a Great Dane from a St. Bernard, nor do domesticated or wild cats differ more from a lion or a tiger than a Pekingese or an English spaniel from an Irish wolfhound. The reason why we hold that all of the varieties of dog belong to only one species is based less on morphological considerations but is rather determined by tradition. It is supposed that all dog breeds are descendants of one or two originally wild forms raised by man in prehistorical and historical times. Even if this be so, it should be of no difference in principle in case we admit the transformation of types as the normal expression of evolution.

When we scrutinize the classification of human characters advanced by Bolk on the basis of his fetalization theory (see above), we recognize that of the primary characters enumerated by that author, only one or two may be claimed to be really of the first order, namely the great weight of the brain and perhaps the hairlessness of the body. As to the others, as the position of the foramen magnum and the persistence of cranial sutures, they are certainly characters of the second order, for they are dependent upon the size of the

brain. Orthognathism, loss of pigmentation and Mongolian fold which Bolk considered as primary are only characters of the third order, for they are not properties of man as such but subject to great variations in the degree of their expression in the different races.

All the morphological peculiarities, the formation of which depends upon other morphological factors, have been classified as characters of the second order. In the case now in question, it can be shown that the brain, or better the size of the brain is responsible for the presence or the special form of the most characteristic features of the skull. Some twenty years ago (1921) in a brief article I showed that the liver is an excellent example of bodily organs with a definite and specific form which, nevertheless, almost entirely depends upon the topographical relation to adjacent organs. The configuration of the abdominal cavity occupied by the liver is determined by shape and arrangement of the ribs, the diaphragm, the stomach and intestine, which together represent a kind of mold of which this organ is, so to say, only a cast. The external tubercle of the human tuber calcanei referred to in the introduction of this article is another example, for its special shape and localization are conditioned by the change in the architectonic structure of the foot which in turn is the consequence of the adaptation to the erect posture. Many years ago, W. Roux anticipating to a certain extent Spemann's later discoveries, advanced the theory that the organism develops by way of self-differentiation as well as dependent differentiation. We now have a much better understanding of those relations. Peculiarities resulting from dependent differentiation are obviously characters of the second order. But it is rather difficult to prove in a given case the true status of any character. In our case, for instance, the question immediately arises whether the enlargement of the brain considered a character of the first order can be interpreted as "self-differentiation."

Before discussing this problem, however, we have to examine the nature of the characters by approaching it from the genetical side. The relative size of the brain in dog determines the presence or absence of certain structural peculiarities of the skull. It is incontestable that both eventualities are hereditary. When we then try to test whether these structural peculiarities belong in the category of genotypical or phenotypical phenomena, we at once realize that none of these terms can be applied to either group of features, since each is a special reaction to the size of the brain which alone appears genotypical for the dog. It is interesting that this reaction is not restricted to one single character but involves a great number covering brain case and face, including even the dentition. The size of the brain, however, is conditioned by the size of the whole body. The size of the body determines, therefore, finally the special appearance of the skull. This fact recalls vaguely the results obtained by Kühne (1932) in studying the inheritance of the variations of the human spine which constitute, as much as I can gather from a report on phenotypy in man by E. Fischer (1939), the only ones available up to date. In this case it could be proved that not the single variation but only the general tendency to produce spine variations of a certain type is inherited.

Julian Huxley (1932) refers to *Cervus elephas* of Scotland as an example of growth relations between body-weight, antler-weight and number of points on the antlers. The antlers can to a certain degree be considered as super-structures of the cranium and their being dependent in size upon the size of the body is strikingly similar to the conditions described above of the super-structures of large animals in contrast to those of small animals. The Scottish stag rarely exceeds 125 kg in body-weight and rarely shows more than twelve

points on its antlers; the usual run of body-weight is only 75–90 kg with six to eight points. In the Carpathian stag the body-weight runs to double the maximum of that of the Scottish deer. A few thousand years ago the skeletons of deer of Scotland matched the largest existing European specimens in size as well as in point-number, according to Ritchie (1920). The relation between body-weight, antler-weight and point-number also holds good for the roe deer (*Capreolus capreolus*) as proved by Dombrowski's figures listed in Table XXXIX and taken from Huxley.

TABLE XXXIX

THE RELATION BETWEEN BODY-WEIGHT, ANTLER-WEIGHT AND POINT-NUMBER OF 405 ROE DEER SHOT IN VARIOUS PARTS OF EUROPE, AFTER DOMBROWSKI

No. of Spec.	Mean Body-Weight in kg	Mean Antler-Weight in g	Mean Point Number
127	16.6	225.7	5.92
254	20.9	257.0	6.05
24	28.3	306.5	6.21

The point-number appears as a function of the absolute antler-size, while the relative weight of antlers increases regularly with the absolute weight of the body. Huxley goes further. According to Thomson (1922) the Scottish red deer was imported more than one hundred years ago into New Zealand and experienced there apparently on account of better environmental conditions a considerable increase of body-weight and as a consequence thereof also an increase of the antler-size and number of their points, the latter running up to twenty and more. In the last years, however "degeneration" set in because of the steady progress in number of deer and the simultaneous destruction of forests with the effect that the body-weight and point-number began to decrease again. From this fact Huxley deduced that "the bulk of the observable differences in size and proportions between the existing Scottish strain of red deer and the existing Carpathian strain and the sub-fossil Scottish type are non-genetic." But more important to me seems the apparent genetical character of the relation between body-weight, on one hand, and antler-size and point-number, on the other, and the increasing or decreasing of the latter in proportion to the former. This inherent quality remained unchanged from early prehistoric times until the present day. It would be interesting to have some positive data also regarding the size or the weight of the brain but it may be supposed that the small deer with small antlers and a low number of points has a relatively larger brain than the large one. In any case, the size of the antler and the number of points are comparable to the supra-orbitals or other super-structures of the cranium for they have to be considered as special characters or characters of the second order.

In our analysis of morphological characters I omitted so far to refer in particular to man in regard to the change these characters have undergone during phylogenetic evolution. All of the most apparent differences in the exterior of the human skull of today when compared with that of gorilla or chimpanzee, serving as an equivalent to the unknown ancestral type, and with *Pithecanthropus* Skull IV as an intermediary form are due to an enlargement

of the brain case and a consequent disappearance of the super-structures and reduction of the face. The enlargement of the brain case in turn is the direct effect of the enlargement of the brain. It has been shown that this whole process can be reversed to a certain extent even in man, if the brain is prevented in early fetal life to grow normally, and thus remains small. Microcephalic skulls, therefore, resemble anthropoid skulls with regard to the special form and aspect of the cranium, form and size of the face and their topographical relation to each other. The respective form of the skull thus can be interpreted as a function of the brain-size.

In dog and other mammals referred to in the preceding pages, the brain-size is in inverse ratio to the body-size. This correlation, however, does not apply to man when compared with the anthropoids, although it holds good within each single group: the pigmy chimpanzee has a relatively larger brain than the normal-sized and men of short stature have relatively larger brains than tall ones. Yet man with his large brain is not the dwarf form of a small-brained anthropoid. This proves that the increase of the human brain is absolute and not relative and must, therefore, be regarded as a true phylogenetic step. It is specific of man as such and represents a fundamental character (character of the first order), while all other morphologic characters of the skull the special appearance of which is only the result of the enlargement of the brain must be ranged under the category of special characters (characters of the second order). They vary in the course of evolution in the degree of development which, in principle, depends upon the actual size of the brain. Considered from the genetical point of view, only the increase of the brain is a genotypic alteration in comparison to the anthropoid phase. As has been shown earlier herein, this modification consists of raising the fetal growth rate of the brain and maintaining it over a longer period.

No other principle seems at work in proceeding from the anthropoid stage of the skull leading to that of man except the general law of relative growth which determines the relation between brain-size and body-size. In dog the fundamental dog character remains the same, regardless of the size of the special variation and the special appearance of the skull. In the case of human evolution discussed above, a fundamental difference seems to exist between gorilla or chimpanzee of our example and man. But it must be borne in mind that we referred to the great apes only for want of the unknown hominid ancestor. That nevertheless remarkable differences actually existed between hominids and anthropoids proper is being made evident with each new discovery. *Pithecanthropus* and *Sinanthropus* reveal specific peculiarities which indicate that the course which led the hominid branch away from the common anthropoid stem was fairly independent of that which yielded gorilla, chimpanzee and orang. To those hominid specialties belong, as far as the skull is concerned, the thickness of the cranium, the development of curious sagittal and horizontal reinforcements of the cranial wall (cf. Weidenreich, 1940 a), the pattern of the teeth, etc.

Now we have to return to the question already broached above, namely what factors may have brought about the absolute enlargement of the brain. In an earlier publication (1924 b) I suggested the adaptation to the erect posture as being responsible for bringing about the preliminary conditions. The effect of the erect posture on the vertical column can best be illustrated by median sections through the trunk as in Fig. 53 (cf. also Fig. 52 in Weidenreich, 1939 b, VI). In apes and even in anthropoids the spine

shows only a slight indication of four sagittal curves (*A*) of which the cervical and lumbar curves are convex ventrally ("lordotic" curves), while the thoracic and sacral curves are convex dorsally ("kyphotic" curves). In man these curves are much more pronounced as a result of the increased stress on the vertebral column as a consequence of the erect posture. It is easy to note that these curves alternate in their direction and thus maintain the balance. As described above, the base of the human skull is deflected at the junction of pre- and postsphenoid (Fig. 54) so that the anterior part of the base is bent downwards.

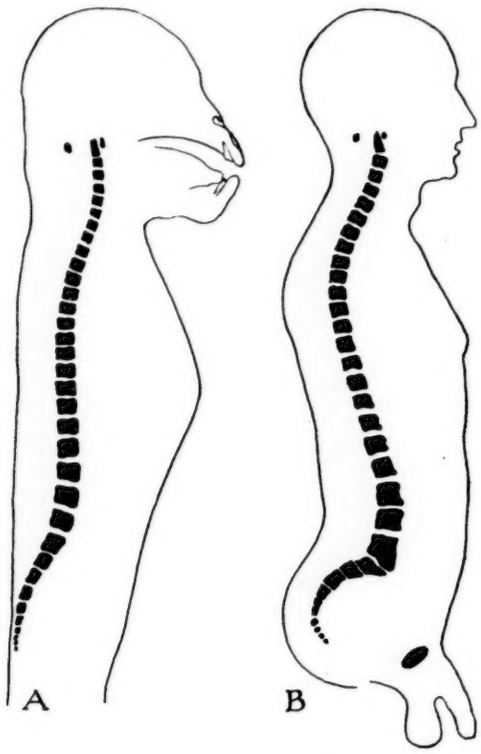

FIG. 53. Median sections through head and trunk of a chimpanzee and man showing the curvature of the spine. *A*. Chimpanzee after Cunningham (1886). *B*. Man after Stratz.

This skull "kyphosis" counterbalances the "lordosis" of the cervical portion of the spine. It brings the face down in adaptation to the new direction of locomotion which otherwise would have been looking upwards had it preserved its original orientation to the spine. No corresponding deflection of the skull base is found in gorilla (Figs. 29 and 34, *B*), chimpanzee or orang (Fig. 52). This change in the orientation of the base favored the expansion of the brain case in dorsal and anterior direction and so provides the necessary space for the brain. That the close correlation between the direction of the basal deflection and that of the spinal curves is of quite general character is proved by the fact that mammals in which the cervical curve is convex dorsally the base is also deflected in opposite direction. This is the case in Cetaceans in which the cervical portion of the spine has become extremely shortened and joined to a functional unity with the strongly kyphotic thoracic region.

The base of the skull represents here a distinct lordotic curve, that is to say, its convexity is directed ventrally (Weidenreich, 1924 b). Dabelow (1929) confirmed the existence of such a correlation, especially for *Phocoena communis* and brings as an additional convincing example the postnatal development of the skull of *Cynocephalus porcarius*. Dabelow's conclusions read: "The facts given and discussed so far confirm rather strikingly Weidenreich's view, that the special figuration of the human skull, in particular the base, must be considered a consequence of the erect posture. They represent, so to say, an *experimentum crucis* carried out by nature which contains the results logically anticipated by Weidenreich's assumption." In spite of his unreserved statement, Dabelow's final results (1931) led him to quite a contrary opinion. He believes that not the erect posture but the growth of the brain is eventually responsible for the special configuration and alteration of the

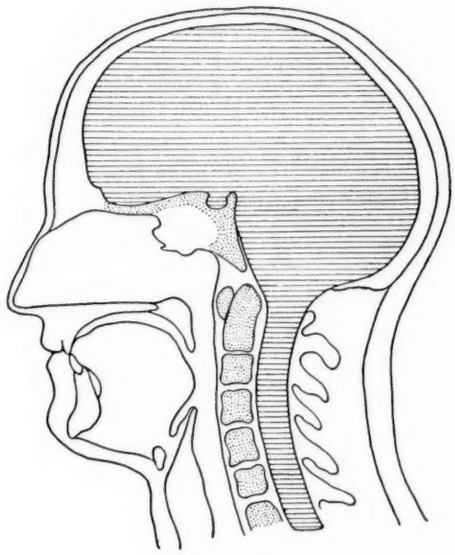

FIG. 54. Median section through a human head showing the dimension of the cranial cavity and the deflection of the skull basis.

skull base. This is not the place to enter into a discussion about this controversy, especially because I have already contended some of Dabelow's arguments in an earlier publication (1934). But since we are dealing here with the decisive rôle played by the brain in the transfiguration of the skull, we must return to that problem. Dabelow found a deflection of the cartilaginous base of the skull already pronounced in fetal stages, even in those animals which never acquire an upright position and in which the deflection becomes lost in the adult stage. Dabelow, a pupil of Bolk, yielded to the same mistake as his tutor in laying special stress on those fetal stages. But it is evident that those stages are only the expression of temporary fetal conditions which within the sphere of the brain are, of course, completely determined by the predominance of its growth rate as discussed in Chapter VII. They change under the influence of definite conditions. As is shown herein, I am more than willing to admit the influence of the brain-size in determining the skull form, but I fail to see how the brain or the brain-size in the case of the Cetaceans could completely

reverse the usual conditions of the cranial base. On the other hand, Dabelow plainly confirms my understanding in the acknowledgment of a close correlation existing between the curve of the cervical region of the spine and that of the skull base. Consequently, the brain would be responsible for all the special curves of the spine, in man as well as in porpoise. This, of course, is entirely out of question. But there is one more cogent reason to prove the improbability of such an assumption. As the finds of *Sinanthropus* reveal (cf. Weidenreich, 1939 b, I and VI), his extremities are much more human-like than the state of the skull and dentition would suggest. With regard to *Pithecanthropus*, it seems rather likely that the same conditions prevailed. The so-called *Pithecanthropus* femur which Dubois attributed as belonging to the Trinil Skull surprises, as is well known, by its completely human-like appearance. Five additional femora very similar to the first one but discovered in later years by the same author remain not less doubtful than it in regard to their real status. But in *Pithecanthropus* Skull IV (cf. Figs. 24–26, *B*) the position of the foramen magnum is markedly more centrally located than in *Sinanthropus*, which condition may indicate, according to an almost universal opinion, that the species designation "*erectus*" once given by Dubois was justified (cf. Weidenreich, 1940 a). If, however, the skeleton of the lower extremity resembles that of recent man remarkably more than the skull does, the conclusion is forced that man had adopted the erect posture long before the cranium had attained its definite size and form or, in other words, the erection of the trunk preceded the special development of the brain. The brain, therefore, can hardly be the direct cause of the erect posture and the special form of the spine. The facts at hand rather point to the contrary.

In the introduction to his study on the lumbar curve of the human spine Cunningham (1886) states that the structural differences between man and the anthropoids are very largely due to man's assumption of the erect attitude, and to his having dispensed with the use of his upper limb as a means of locomotion. The author continues: "Thus the upper limbs are shortened, whilst the lower limbs are lengthened and strengthened, and possess the power of being fully extended at the hip- and knee-joints. There is not one region of the body in which modifications in structure to suit this characteristic posture may not be found." Indeed, if we examine the human skeleton, we are again and again surprised to see to which extent form and size of the individual bones conform to each other and to the construction as a whole. Thus, the idea suggests itself that most of these characters must owe their special shaping to other, really responsible factors. In the case of the skull, it is the size of the brain which determines its special configuration and the particular appearance of the individual features. As to the special characters of spine and lower extremity, the acquisition of the erect posture appears here as the decisive factor. It affects even such relatively minor details as position and form of the external tubercle of the tuber calcanei (Weidenreich, 1921/22, 1940 b). The realization of these relations is of essential importance for a correct conception of the process of phylogenetic evolution. For it shows that the original constitution of only very few fundamental characters must be changed to set in motion the alteration of the entire machinery of special characters. Böker (1936) very correctly recognized this fact. In "a great number of cases" he states, "there is the possibility to alter many characters simultaneously merely by one step of mutation by means of heterogonic growth of individual organs as compensatory effects, and pleiotropy of the genes, respectively." So far as the growth of the brain is concerned,

it is easy to fix the point or the organ in which the change sets in. The acquisition of erect posture, however, is more difficult to localize. There is, of course, no organ in which this attitude is, so to say, chiefly concentrated, for it appears as a reaction of the whole organism which affects the skeletal as well as the muscular system. Yet each change could be brought about by altering the relative rates of growth of all parts concerned. All this will only make sense, if the organism is interpreted not as a conglomeration of single independent elements, may they be organs or cells, but as a totality.

Therefore, even the most complete knowledge of the hereditary behavior of a single peculiarity is not able to contribute much to the understanding of nature and mechanism of evolution, especially if this peculiarity is one of the third order. For evolution consists of a continuous and simultaneous alteration of fundamental and special characters which together represent in all stages a definite morphological unity.

Human evolution, as far as it is expressed in the increase of the brain and in the transformation of the skull, appears under the form of orthogenesis. This can be deduced from the mere fact that the alteration of the morphological features of the skull correspond exactly to such different forms characterizing the series of skulls of small and large animals and their intermediary stages. That the enlargement of the brain itself proceeds in a definite

TABLE XL

THE RELATION BETWEEN CRANIAL LENGTH AND FACIAL LENGTH OF THE THREE ANCESTRAL GROUPS OF *Equus*, AFTER ROBB (1935)

	Skull Length	Face Length	Cranial Length	Facial Index Average
Group I	11.5–17.8	5.2– 9.7	6.3– 8.1	0.95
Group II	17.2–23.0	8.5–12.0	8.7–11.0	1.035
Group III	46.5–62.0	28.8–39.5	17.5–24.0	1.59

direction can be proved by the following three facts: (1) the gradual enlargement of the brain is specific of the entire primate group, (2) the different phases of the phylogenetic line represented by *Pithecanthropus*, *Sinanthropus*, Neanderthal Man (*Homo soloensis*, Rhodesian Man) and Modern Man reveal the tendency to progressively increase the cranial capacity and simultaneously to reduce the super-structures and the face; (3) the changes may be brought about by a gradual alteration of the growth rate, that is to say, by retaining the original fetal rate over an ever more extended period.

The entire process is analogous to the evolution of the skulls of *Equus* and *Titanotherium*. According to Robb (1935), in the phylogenetic development of *Equus* there is a progressive facial preponderance concomitant with the increasing size of skull and body. Robb divides the ancestral forms into three groups: the first comprises the representatives of the types with four toes, the second those with three toes and the third those with one toe. In Table XL skull length, face length, cranial length and the index of the two latter measurements are listed. These figures show that the share of the face, indeed, increases with the increase of the size of the skull and the body as is also apparent in the illustration given in Fig. 55. Robb, furthermore, shows that this phylogenetic process is identical

to that which occurs in the ontogenetic development of the skull. His results, demonstrating the increase of the facial index during ontogenetic development, are given in Table XLI.

Although in this case the relative size of the brain and its influence on the size of the face are not as pronounced as in the human evolution or in dogs, it is evident that the principle governing this relation is the same. Its correspondence to body-size is likewise obvious. Robb's conclusions are similar to my own as follows from his statement: "Continuous evolution in the shape of the horse skull did not occur except as a concomitant of the one hundred-fold increase in total mass. Given that size is in large measure genetically determined, it is possible to describe the evolution of form in terms of genes augmenting total size. Progressive pre-optic preponderance in the horse is a by-product of whatever factors have permitted size increase in the progeny of *Eohippus*." But Robb denies the existence of orthogenetic trend in the evolution of the equine skull. Orthogenesis should only be

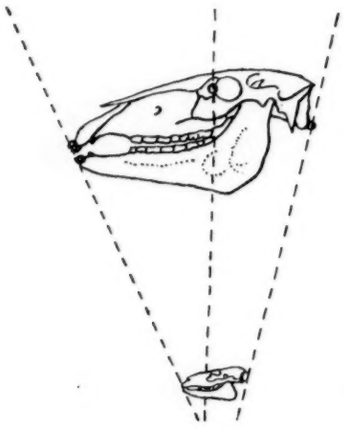

FIG. 55. Evolution of the horse skull (*Eohippus* below, *Equus* above) to demonstrate the progressive pre-optic preponderance. After R. C. Robb (1935).

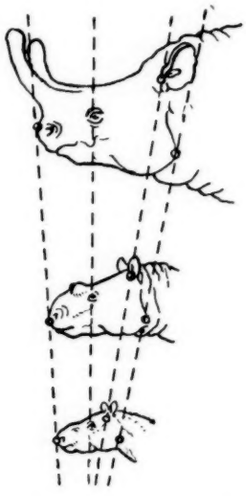

FIG. 56. Evolution of *Titanotheres* (*Eotitanops* below, *Manteoceras* in the middle, *Brontotherium* above) to demonstrate the progressive post-optic preponderance. After R. C. Robb (1935).

feigned by the attainment of successively greater adult size by the more recent genera, and this should be due to a fortuitous occurrence probably aided by some natural selection. On the contrary, I consider precisely the continuous increase of body size characterizing and determining the entire phylogenetic development of the horse as a typical case of orthogenesis.

In Titanotheres the conditions are similar but still more characteristic, for here the phylogenetic increase of skull and body size is combined with the successive development of a frontal horn (Fig. 56). According to Osborn (1929), the frontal horn is not to be found in the earliest and smallest ancestral forms but makes its appearance as a low elevation in later stages and ends with a large bifurcated horn in the last representatives of the type. Osborn distinguishes four lines of descendants which differ in certain peculiarities but display the same phenomena with regard to the horn. He, therefore, considers the evolution of Titanotheres as an example of true orthogenesis. Julian Huxley (1932) refers to this

particular case. He admits the surprising fact that the mechanism for horn-growth must have already been prepared in the germ-plasm before any of the Titanotheres was large enough to produce a horn. Furthermore, any adaptive value to the horn must be completely excluded for the early stages of the evolutionary development, because the horns in these cases have been represented only by the merest incipient knots or still more have existed merely potentially. In spite of this admittance, Huxley contends the necessity to invoke orthogenesis—provided that within the germ-plasm of the Titanothere ancestor there existed a hereditary basis of growth mechanism for a frontal horn, and was advantageous for this type in general. But, in my opinion, the orthogenesis is less defined by the predestination of the horn than by the simple fact that the entire phylogenetic evolution of the Titanotheres is achieved in the form of a constant increase in size and that the gradual development of super-structures is inevitably bound to this enlargement of

TABLE XLI

THE RELATION BETWEEN CRANIAL LENGTH AND FACIAL LENGTH IN THE ONTOGENETIC DEVELOPMENT OF THE HORSE, AFTER ROBB (1935)

Age	Skull Length	Face Length	Cranial Length	Facial Index
Fetus 5–6 months	15.2	7.9	7.3	1.08
Fetus 10 months	26.4	15.4	11.0	1.36
Newborn	33.8	20.5	13.3	1.54
11 months old colt	48.2	29.3	18.9	1.55
3½ years old horse	51.7	31.3	20.4	1.54
Gelding truck horse (adult)	56.5	36.0	20.5	1.76

body and skull. In the case in question, a horn is a special requisite of the equipment of Titanothere. In relation to the skull, it appears as a super-structure and will consequently behave like such if body and skull increase in size manifesting the special phylogenetic development of this type.

As has been shown, the characters of the body can be divided into three categories of which, however, only those of the first order are essential to the problem of evolution. Characters of the second order appear as directly dependent upon the first and thus have no real significance if viewed from the phylogenetic standpoint; they can be understood only in connection with the first. Characters of the third order are but of secondary significance inasmuch as they are at best only loosely connected with the fundamental character of the type. They are important for the definition of species, subspecies and races but have no decisive bearing on the problem of evolution itself. But precisely these secondary characters constitute the basis for genetical experiments, for those of the first order are absolutely inaccessible to them. As long as such conditions persist—I fear, forever—genetical experiments can contribute but little to the advancement of our knowledge of phylogenetic evolution. Such an advancement can be realized only by a close collaboration of comparative anatomy and palaeontology.

CONCLUSIONS

Cranial sutures in recent man show a tendency to fuse relatively late in life when compared with anthropoids in which they close and even become partly obliterated shortly

after the second dentition is completed. The suture of all the three adult *Pithecanthropus* skulls now available, especially Skull IV, exhibits such a state of closure as is scarcely attained in recent man, or if at all, at a rather advanced age. However, the preserved dentition of Skull IV shows so slight a degree of wear that this individual must have been relatively young. Therefore, it is justifiable to assume that the cranial sutures close earlier in *Pithecanthropus* than in recent man, and in this respect approximate the conditions in anthropoids. Bolk found that in small monkeys, especially within the platyrrhine group, the sutures are much less inclined to close, whereas in large apes and anthropoids they fuse early and in man again they do so much later. In placing Max Weber's data on the relation between brain-weight and body-weight against Bolk's results who attempted to express in figures this tendency towards suture closure, the parallelism becomes striking. This fact suggests that persistence or early obliteration of the cranial sutures is correlated in some way with the relative size of the brain.

The skull of the dwarf dog (Pekingese, Bolognese, English spaniels, etc.) differs from that of large ones (wolfhound, St. Bernard, Newfoundland, etc.) not only in size but also in form and proportions of the two constituents of the skull, cranium (brain case) and face. Only the skull of the large type shows the features considered characteristic of genus *Canis*, namely a long and narrow form with the cranium proper relatively small but carrying heavy super-structures (postorbital process and sagittal and nuchal crests) and the face (the jaws) far projecting. As to their topographical relations, the cranium and face (upper jaw) are oriented in a straight line, the cranium behind and the face in front with a large frontal air sinus inserted between the anterior end of the cranial cavity and the nose. The skull of a dwarf dog, however, is short and broad with the cranium enormously enlarged and the face greatly reduced, so that the cranium assumes the form of a globule with super-structures and frontal sinus missing, while the face has shifted backwards to lie under the anterior part of the cranium. One of the most surprising features of the cranium is the persistence of the cranial sutures and occasionally even of the fontanels which may remain patent until the end of life. These differences can be traced back to the general knowledge that small animals have relatively larger brains than large animals. But the morphological consequences have constantly been overlooked, namely that the large brain occupies a relatively much larger space in the generally reduced skull of dwarfs than the proportionally small brain in the large skull of large types. Hence the cranial cavity of the former tends to expand as widely as possible. In typical cases (large types) the frontal bone participates in the formation of the brain case only with its posterior end, while in dwarfs it partakes in its entirety, so that the cranial cavity extends forwards and downwards to the nasion. Since the brain case simultaneously increases in breadth and height, all of the bony substance available for the formation of the walls appears exhausted and thus insufficient to meet the requirements. Hence the retardation in suture closure and persistence of fontanels. This is in close conformity with the fact that the walls of the brain case in dwarf dogs are considerably thinner than in large types.

The enlargement of the brain case results in an extensive reduction of the face. This manifests itself not only in a shortening of the face but also in its lowering, while its breadth remains unchanged. Consequently, the palate and dental arch become short and wide instead of long and narrow as in the type. The teeth are also affected by the alteration. The size of crowns and roots is greatly diminished and, in extreme cases of dwarfism, not

only are premolars and molars reduced in number but their patterns also have undergone a remarkable simplification consisting in the loss of the cingulum and even of certain cusps. The reduction of the entire masticatory apparatus, in close connection with the enlargement of the brain case, fundamentally alters their mechanical correlations. If the brain case is small but the masticatory apparatus large, the cranial surface is not sufficiently expanded to provide the necessary space for the attachment of the massive musculature and not strong enough to withstand the chewing force. In consequence of this disproportion, the cranial surface becomes enlarged and strengthened by super-structures like the sagittal and nuchal crests and the postorbital process. If the brain case is large but the masticatory apparatus small, the cranial surface is large enough to accommodate the reduced muscles and at the same time strong enough to serve as a buttress for the diminished chewing force which, in addition, attacks at a more posterior level, as the result of the changed topographical relation between brain case and jaws. Since from the architectonical standpoint air sinuses are regions left vacant between the mechanically essential pillars of the constructing parts of the face and cranium, they become smaller or disappear completely with the decrease in incongruity between the individual constituents of the skull.

That the described differences in form, proportions and construction of dog skulls are not merely incidental occurrences but the expression of strict correlations of general validity, is supported by the facts (1) that there is a continuous line of dog types from the largest to the smallest in which all intermediary stages occur, and (2) that the same situation is realized in other groups of mammals wherever small types contrast to large ones, although the degree of the divergence may vary. Among the Felidae the wild or domesticated cat, as representative of the dwarf type, differs from lion or tiger in regard to the relation between brain case and face in almost the same way as in dog. The same holds good for marmosets, on the one hand, and howler monkeys or Cercopithecidae, on the other. All of the morphological differences between the skull of the pigmy chimpanzee (*Pan paniscus*) and the normal-sized chimpanzee (*Pan schweinfurthi*) can be traced back to the same cause, namely that the dwarf type has a relatively larger brain and brain case than the normal-sized ones. The dwarfs invariably also show a distinct tendency towards a later closing of the cranial sutures.

The phylogenetic evolution of the human skull is characterized by a continuous enlargement of the brain. The morphological effect of this enlargement corresponds completely in principles and details to that which is seen in the dwarf dog, as a consequence of its relatively larger brain. If we assume that the immediate ancestor of the human line in general appearance of the skull and in the proportion between brain case and face resembled one of the present-day apes—a supposition perfectly justified by the skull characteristics of the prehominids *Pithecanthropus* and *Sinanthropus*—this anthropoid-like ancestor, as personified by the gorilla, for instance, in our parallel, would take the place of the large type of dog, and modern man that of the dwarf with the prehominids ranged intermediate. In the first the brain case proper constitutes the smallest portion of the skull and the face the largest, while in the second the conditions are completely reversed. The super-structures (supra-orbitals, sagittal and nuchal crests) in the supposed anthropoid ancestor are of an enormous size, especially in male individuals, while in man they have completely disappeared. The cranial cavity of the gorilla does not extend up to the glabella region and a spacious air sinus occupies the entire space between the anterior end of the cranial cavity

and the glabella. In modern man the frontal bone is in erect position and bulging, the cranial cavity extending to the glabella region, and the air sinus is small. In correspondence therewith the brain case expands in height and breadth due to the tendency of assuming a globular form. While in anthropoids the cranial sutures close rather early in life, in modern man they remain patent. The persistence of the metopic suture not infrequently observed in man but rarely seen or completely absent in anthropoids, represents only a special case of this general tendency. The arrangement of the pterion sutures also seems to be conditioned upon the expansion of the brain and the erect position of the forehead, since the anthropoid pattern (frontal-temporal contact) is characterized by a flat and lowered frontal bone while the human pattern (parietal-sphenoidal contact) by a more bulging and erect one. The pigmy chimpanzee, therefore, in which the latter condition is realized exhibits the human pattern in contrast to the normal-sized chimpanzee.

The face of the anthropoids is characterized by its excessive size in proportion to the brain case; it exhibits a pronounced prognathism, an enormously developed mandible, a long and narrow palate and dental arch, and a powerful dentition. The face of modern man is rather small in proportion to the brain case: it is less orthognathous; the jaws are reduced in length, height and bulkiness; palate and dental arch are short and wide; and the dentition is weak. The topographical relation between brain case and face has undergone a characteristic change. In anthropoids only the posterior part of the face is covered by the brain case, while its major portion protrudes far beyond the anterior pole of the latter. In man the brain case is superposed upon the face as a consequence of the enlargement of the former as well as of the reduction of the latter. The orbit the walls of which are mainly formed by the facial skeleton is larger in anthropoids than in man. In other words, the disproportion between the size of the eyeball and the volume of the orbit is greater in the former than in the latter. The teeth, when compared with those of the anthropoids and even with those of *Sinanthropus*, show not only a considerable reduction in size, especially the frontal teeth, but also a marked simplification of the pattern. The cingulum and the wrinkles are lost and the cusps, particularly those of the lower molars, exhibit a tendency to a reduction in size and number.

Pithecanthropus and *Sinanthropus* stand intermediate with regard to all these peculiarities, though certain features come closer to those of man. This also applies to the size of the brain. The average cranial capacity of gorilla amounts to about 475 cc, that of *Pithecanthropus* and *Sinanthropus* to 900 and 1000 cc, respectively, and that of modern man to about 1300 cc.

To what extent the brain size determines the form and proportions of the skull even in modern man is revealed by the peculiarities of microcephalics. If in such cases the cranial capacity is reduced to less than one-third of the norm, the form of the brain case approaches that of a "Neanderthal" type with flat and receding forehead, occasionally with real supra-orbitals and large air sinuses, and with the temporal lines approaching the sagittal suture. The face, however, develops to an almost normal size and thereby recalls conditions existing in anthropoids: the face in relation to the brain case is much larger than in the norm; it is not covered by the brain case but protrudes considerably beyond the anterior pole of the latter; and the palate and dental arch appear elongated and narrow. The real reason for microcephaly is unknown, but if the normal growth of the brain is arrested in early fetal life causing the brain case to remain small, while the growth of the

face is less affected, the two constituents display again the primary disproportion which characterizes the earlier stage of human evolution.

The view frequently expressed that muscular pressure or similar forces acting under conditions of normal growth affect size and form of the brain case and through this medium the brain itself cannot be confirmed by experiments. On the contrary, all the facts now on hand prove that those mechanical influences can only affect the development of the super-structures but not the cranium itself and still less the brain. Abnormal cranial forms like scaphocephaly and others are not the result of premature obliteration of the cranial sutures but, on the contrary, the sutures close earlier on account of the abnormal conditions of the brain.

The explanation offered for the fact that small animals have relatively larger brains than large types has made very little progress since the question was first raised. Dubois' "cephalization-coefficient" failed to supply a mathematical formula for the "psychical factor" serving as an estimation of the predominance of the brain volume of one or the other species or group. Dubois calculated this coefficient (k) on the basis of the formula: $E = kS^r$ in which E is brain-weight and S body-weight while r represents the relation exponent between the quantity of the brain and the surface of the body. According to Julian Huxley, Dubois' formula is equivalent to the general allometric formula: $y = bx^\alpha$, in which y is brain-weight, x body-weight, α the "equilibrium constant" and b (Dubois' cephalization-coefficient "k") the "initial growth index." The value of b (k) is largely dependent upon the value of r. Dubois claims that r (α) should be the same for all mammals, including man and amount to 0.56. But so far as man is concerned, the determination of the cephalization-coefficient seems rather doubtful. Dubois computed this coefficient on the basis $r = 0.56$, to 2.822 for male and 2.818 for female, while the corresponding figure for orang-utang should be 0.753 and for *Symphalangus syndactylus* 0.770. Yet r (α) is not equal for all mammals. For instance, it is 0.23 for dog and, according to another publication by Dubois, 0.25 for man. If r is computed on the basis of a comparison between man and chimpanzee and not between orang and siamang, as done by Dubois on the assumption that r is the same for all mammals, one will find $r = 1.32$. If $r = 0.25$ (Dubois' second computation), then the cephalization-coefficient rises to 86.8 for males and 81.7 for females; if $r = 1.32$, however, the coefficient falls to 0.00636.

The fact remains certain that man has a large brain in relation to the size or the weight of the body, namely an average of 1 : 46 for male and 1 : 42 for females (according to Dubois), implying that the latter have a relatively larger brain than the former. This may explain to a certain extent the sex differences between male and female skulls, the latter having a more globule-shaped cranium and a relatively smaller face. The more globular shape of the cranium explains the fact that the cranial index of females is always slightly higher than that of males within the same population. The relatively larger brain of the female when compared with the male is in correlation with her generally smaller stature. Tall individuals have relatively smaller crania than short ones, or pigmies and dwarfs have larger crania than normal-sized individuals.

Form and proportions of the skull of modern man when compared with that of gorilla or a prehominid correspond to a dwarf type in which the brain is large in relation to the size of the skull. In the course of evolution, the brain could, therefore, become enlarged if the body-size had correspondingly been reduced. The real course, however, shows that

the consequences of the enlarged brain with regard to the transformation of the skull have been, it is true, applied to man, but there is no evidence of a simultaneous reduction of the body-size. For the prehominids were already of the same stature as modern man. In other words, the enlargement of the human brain is not a relative but an absolute one, that is to say, phylogenetic evolution consists of a continuous increase in brain volume, and the transformation of the human skull is merely a result thereof.

Bolk advanced the theory that man must be considered a primate fetus which has become mature, in other words, the original fetal features are permanently preserved in man but lost in anthropoids. This should be the reason why embryos and young individuals of great apes and man bear a much closer resemblance to each other in form and size of the cranium than at adult stage. Bolk, therefore, characterized the development of man as "conservative" and that of the anthropoids as "propulsive." The skulls of newborn puppies of dwarf and large dogs fail to show any difference in form and proportions; in the first case, however, the proportions are preserved during the post-natal development, while they disappear in the latter. Therefore, in the ontogenetic development also there exists a complete parallelism between dwarf dogs and man and anthropoids and large dogs. But to say that the conditions as seen in man and dwarf dogs are due to the retention of fetal features is misleading. What really has been preserved in man (and in dwarf dogs) is the fetal growth rate of the central nervous system which implies the predominance of the brain over the other organs during the greater period of fetal life. In anthropoids the fetal growth rate of this system, though lower than in man, nevertheless exceeds also that of the other organs, hence the closer resemblance of man and apes in early life. But the growth rate decreases gradually in the subsequent stages of ontogenetic development until it comes to a standstill. In anthropoids this stage is reached somewhat earlier than in man and at a time when the growth of the face is still more active. The anthropoid development thus seems "propulsive" and that of man "conservative" if the growth of the face is considered the essential point, but it is reversed if the growth of the brain is regarded as decisive. The "fundamental difference" between man and anthropoids which Bolk deduced from their different appearance in adult stages and their greater similarity in young ones proves to be nothing more than an increased growth rate of the human brain and a retardation in its differentiation in anthropoids. This difference is of the greatest importance but has no "fundamental character" in the sense of Bolk.

The correlation between brain-size and body-size or between cranium and face is only one example of the organism representing a unit of independent and dependent differentiations. The morphological characters, therefore, are not all of equal validity when serving as indicators for the determination of the systematic position of a given organization, its nature and the course of its phylogenetic evolution. Viewed from the latter standpoint, three categories of characters can be distinguished: characters of the first order are those which are fundamental and define the basic organization (family, for instance). In our example of dogs, they are manifest in the general canine nature, regardless of size or race. Characters of the second order are such as define the special appearance of the type. In the case of dogs, the special form and peculiarities of the skulls of a Pekingese, on one hand, and an Irish wolfhound, on the other, are characters of the second order. In the case of Felidae, the feline characters of cat and lion or tiger fall within the first order; the differences in size, form and proportion of the skull constitute special characters or those of the

second order. Characters of the third order include those which have no direct relation to the fundamental and special nature of the type and are with regard to these characters of secondary significance. In the example of dogs, these concern the texture and color of the hair, the length of the ear and tail, etc.; in the case of the Felidae, the differences in the appearance of lion and tiger, for instance, exclusively concern the distribution of hair and coloring. Such characters form the basis mainly when defining species, subspecies and races, and constitute the major factors underlying genetical experiments since really fundamental characters are not accessible for such experimentation.

The phylogenetic evolution of man, at least in its late phases is characterized by the absolute increase in brain size. The brain size, therefore, represents a character of the first order but all the peculiarities of cranium and face which result from the enlargement of the brain and are generally considered the most essential indicators of evolutionary progress are characters only of the second order. Characters of the third order like texture of hair, dark and light pigmentation of hair and skin, thick and thin lips, straight and arched noses have no bearing on the problem proper of human evolution, regardless of whether they represent genotypic or phenotypic phenomena. If the phylogenetic enlargement of the brain constitutes a genetic change of the type—which undoubtedly is the case—this change alone is sufficient to transform "automatically" the entire skull with all its peculiarities. Since the enlargement of the brain appears as the inducing cause of other morphological alterations, the question is justified as to which general factor may now be made responsible for this enlargement. It can be reasonably assumed that the adoption of the upright posture was accompanied by characteristic changes in structure and proportion of the trunk and all constituents of the lower extremity, particularly also in the static and dynamic conditions of the spine. The increasing deflection of the base of the human skull which appears as the result of the special curvature of the spine supplied the possibility of widening the brain case and thereby the space to house the enlarged brain. It is rather difficult, of course, to distinguish sharply in this instance between cause and effect because each individual part concerned acts upon the other. But the enlargement of the brain is certainly in some way connected with the adoption of the erect posture and the corresponding transformation of the entire skeleton.

All the facts imply that phylogenetic evolution of man proceeds under the form of an orthogenetic development. The tendency to enlarge the brain accompanying the acquisition of higher organization is characteristic of the primate group as such. In spite of the deficiency of the available fossil material, it nevertheless is evident that the mass of the brain has increased with every new step taken in the direction leading to recent man, and that as a consequence of the general law which determines the growth relation between brain case and face and proved to be unalterably valid for each evolutionary phase, the transformation of the skull could only take the general course which it actually has taken. In other words, it is an example of orthogenetic development.

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PHYLOGENETIC AND CYTOLOGICAL STUDIES IN THE RANUNCULACEAE

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INTRODUCTION

The Ranunculaceae, as a natural order of plants, have been recognized for over two hundred years. It was not until 1789, however, that A. L. de Jussieu adequately delimited them as a valid taxonomic unit. Since that time numerous contributions have been made to their classification, phylogeny, morphology, anatomy, and cytology. Although the family has been long known and many of its genera are among the oldest recognized native plants of Europe, considerable confusion still persists as to the number of genera and species. In general the family consists of about 30 genera and 1200 species widely scattered over the earth, to the limits of vegetation on high mountains and towards the poles but is comparatively rare in the southern hemisphere and in the tropics (Hutchinson 1926). Some of the various estimates as to the number of genera and species are as follows: Bailey (1930) Hortus—50 genera; Engler and Gilg (1924) Syllabus der Pflanzenfamilien—1200 species; Willis (1925) Flowering Plants and Ferns—40 genera, 700 species; Britton and Brown (1897) Illustrated Flora—35 genera, 1050 species; Bailey (1925) Manual of Cultivated Plants—30 genera, 1200 species; Rehder (1935) Cultivated Trees and Shrubs—48 genera, 1300 species; Johnson (1931) Taxonomy of the Flowering Plants—35 genera, 1200 species.

Its nearest relatives are the Ceratophyllaceae, the Magnoliaceae, Nymphaeaceae, Calycanthaceae, Anonaceae, Menispermaceae, Berberidaceae, and Lauraceae in the Dicotyledons and the Alismaceae and perhaps other members of the Helobeae in the Monocotyledons.

The family is characterized, according to Prantl (1891), by spiro-cyclic, seldom completely cyclic flowers with simple calyx to calyx and corolla; in the first instance calyx frequently with nectaries located between the calyx and the stamens; mostly perfect, actinomorphic, seldom zygomorphic. Stamens mostly numerous, free. Carpels 1–many, mostly free, seldom united, with 1–many seeds. Integuments 1 or 2. Fruit a follicle or achene, seldom a berry. Endosperm oily with small embryo. Pollen formation simultaneous, pollen mostly 2-nucleate, seldom 3-nucleate. Perennial, annual; mostly herbs, subshrubs, and vines.

A few of the major taxonomic treatments of the Ranunculaceae after Jussieu have been those of de Candolle (1824), Bentham and Hooker (1862–67), Baillon (1863), Prantl (1888) and (1891), Engler and Gilg (1924). Other numerous works on morphology and anatomy, and monographs on individual genera have added considerable knowledge as to form, structure, life habit, geographical distribution, and new species within the family but have not altered greatly the basic lines of classification as outlined by Prantl (1888) and Engler and Gilg (1924).

De Candolle (1824) arranged the family in five tribes under what he called the order Ranunculaceae Juss.

Tribe I. Clematideae:
Clematis, Naravelia
Tribe II. Anemoneae:
Thalictrum, Tetractis, Anemone, Hepatica, Hydrastis, Knowltonia, Adonis
Tribe III. Ranunculeae:
Myosurus, Ceratocephalus, Ranunculus, Ficaria
Tribe IV. Helleboreae:
Caltha, Trollius, Eranthis, Helleborus, Coptis, Isopyrum, ?Enemion, Garidella, Nigella, Aquilegia, Delphinium, Aconitum
Tribe V. ?Paeoniaceae: (Ranunculaceae spuriae)
Actaea, Zanthorrhiza, Paeonia

Bentham and Hooker (1862–67) grouped the genera somewhat differently into the same five tribes.

Tribe I. Clematideae:
Clematis, Naravelia
Tribe II. Anemoneae:
Thalictrum, Anemone, Knowltonia, Adonis, Callianthemum, Myosurus
Tribe III. Ranunculeae:
Trautvetteria, Ranunculus, Hamadryas, Oxygraphis
Tribe IV. Helleboreae:
Subtribe Caltheae:
Caltha, Calathodes, Glaucidium, Hydrastis, Trollius, Helleborus, Eranthis
Subtribe Isopyreae:
Coptis, Isopyrum, Nigella, Aquilegia, ?Anemonopsis
Subtribe Delphinieae:
Delphinium, Aconitum
Subtribe Cimicifugeae:
Actaea, Cimicifuga, Xanthorhiza
Tribe V. Paeonieae:
Paeonia

Baillon (1863–64) confused the classification of the genera somewhat and divided the family into four series corresponding to the tribes above.

Series A. Ancolies:
Aquilegia, Xanthorrhiza, Nigella, Isopyrum, Helleborus, Trollius, Delphinium
Series B. Renoncules:
Ranunculus, Myosurus, Anemone, Callianthemum, Hydrastis
Series C. Clematites:
Clematis, Thalictrum, Actaea
Series D. Pivoines:
Paeonia, Crossosoma?

Prantl (1888) and (1891) divided the family into three tribes. Two of the tribes, viz. Paeonieae and Helleboreae, are characterized mainly by follicular fruits with many seeds; whereas the third tribe, Anemoneae, is characterized by 1-seeded achenes. The Paeonieae is differentiated from the Helleboreae by having the outer integument longer than the inner, flowers mostly single, no nectaries, and a fleshy ovary wall.

Tribe I. Paeonieae:
Glaucidium, Hydrastis, Paeonia

Tribe II. Helleboreae:
Caltha, Trollius, Callianthemum, Helleborus, Eranthis, Nigella, Leptopyrum, Isopyrum, Coptis, Xanthorrhiza, Anemonopsis, Actaea, Aquilegia, Delphinium, Aconitum

Tribe III. Anemoneae:
Anemone, Clematis, Myosurus, Oxygraphis, Trautvetteria, Ranunculus, ?Hamadryas, Thalictrum, Adonis

Lotsy (1911) omitted Prantl's tribe Paeonieae and considered its genera not members of the Ranunculaceae. He raised the rank of Prantl's other two tribes to that of subfamilies and further divided the family into tribes and subtribes.

Subfamily Helleborioideae:
Tribe I. Isopyreae:
Subtribe Helleborinae:
Helleborus, Eranthis
Subtribe Isopyrinae:
Leptopyrum, Isopyrum, Aquilegia
Subtribe Cimicifuginae:
1. *Anemonopsis, Cimicifuga, Actaea*
2. *Coptis, Xanthorrhiza*

Tribe II. Trollieae
Subtribe Trollininae:
Trollius, Callianthemum, Caltha
Subtribe Nigellinae:
Nigella (*Komaroffia*)
Subtribe Delphiniinae:
Aconitum, Delphinium

Subfamily Anemonoideae:
Subtribe Anemoninae:
Anemone (with *Knowltonia*)
Thalictrum (with *Anemonella*)
Subtribe Clematidinae:
Clematis
Subtribe Ranunculinae:
Myosurus, Trautvetteria, Ranunculus (with *Ficaria, Ceratocephalus,* and *Batrachium*), *Adonis*

Engler and Gilg (1924) retained the classification of Prantl (1891) with the exception of removing *Glaucidium* and *Hydrastis* from the tribe Paeonieae and creating a fourth tribe, the Hydrastideae. As will be shown later this change was well founded from the standpoint of cytology.

The first significant alteration of these schemes of phyletic arrangment was made when Langlet (1932) published his arrangement of the genera based on chromosome studies of over 200 species representing most of the genera in the family. Previous to this work Langlet (1927) had published his account of chromosome numbers in the Ranunculaceae. Up until this time very little was known concerning the chromosomes of the family and nothing was known concerning their taxonomic importance. The principal contributions to the cytology of the Ranunculaceae from the standpoint of individual genera have been those of Afifi (1933) and Schafer and La Cour (1934) on *Aconitum;* Moffett (1932) on *Anemone;* Skalinska (1928), (1935), and (1938) on *Aquilegia;* Lindsay (1929) and (1930), Polinkova (1936), and Meurman and Therman (1939) on *Clematis;* Tjebbes (1927) and Lawrence (1936) on *Delphinium;* Sax (1932), Hicks and Stebbins (1934), Dark (1936), Sax (1937), Sinoto (1938), Stebbins (1938), and Stebbins and Ellerton (1939) on *Paeonia;* Sorokin (1924), Senjaninova (1926), Sorokin (1927), Whyte (1929), Jane (1932), Larter (1932), Flovik (1936), Coonen (1939), and Flovik (1940) on *Ranunculus;* Kuhn (1928), (1930), and (1933) on *Thalictrum.* Cytological contributions of a more general nature, i.e. on the entire family or large sections of the family have been those of Hocquette (1922), Langlet (1927) and (1928), Lewitsky (1931) and Langlet (1932). Of these works, Lewitsky (1931) and Langlet (1932) are of especial importance from the standpoint of systematics and phylogeny.

Lewitsky's contribution (1931), although of the highest theoretical and practical importance for the relationship of systematics and the "karyotype" did not offer any profound reorganization of the phyletic arrangement of the genera within the Ranunculaceae. Langlet on the other hand, challenged the foundations of the systematic schemes in the classic works referred to above. In his studies Langlet (1927) noticed that the chromosomes fell into two sharply and markedly different groups based on both size and "type" of the chromosomes. One type he described as predominantly large, always long and bent and called it the Ranunculus type (R-type). The second type he described as small and kidney-shaped and called it the Thalictrum type (T-type). Using Lotsy's phyletic scheme of the family as a basis of classification Langlet (1932) divided the Ranunculaceae into two subfamilies as differentiated by the type of chromosomes.

Subfamily Thalictroideae (T-type)
- Tribe I. Thalictreae
  - Subtribe Isopyrinae:
    - *Isopyrum, Leptopyrum, Aquilegia*
  - Subtribe Thalictrinae:
    - *Thalictrum, Anemonella*
- Tribe II. Coptideae:
  - *Coptis, Xanthorrhiza*

Subfamily Ranunculoideae (R-type)
- Tribe III. Helleboreae

Subtribe Helleborinae:
Helleborus, Eranthis
Subtribe Cimicifuginae:
Anemonopsis, Cimicifuga, Actaea
Tribe IV. Ranunculeae:
Myosurus, Trautvetteria, Ranunculus
Tribe V. Anemoneae
Subtribe Anemoninae:
Anemone, Knowltonia
Subtribe Clematidinae
Clematis
Tribe VI. Trollieae
Subtribe Trolliinae:
Caltha, Trollius
Subtribe Delphiniinae:
Delphinium, Aconitum
Tribe VII. Adonieae:
Callianthemum, Adonis
Tribe VIII. Nigelleae:
Nigella, Komaroffia

The present investigation is designed to re-examine the validity of such a reclassification of the Ranunculaceae from a cytological standpoint and to evaluate if possible, the relative effects of some of the different forces at work within the family on speciation and evolution.

Materials and Methods

Nineteen genera representing all of the subdivisions of the family except those represented by *Hydrastis-Glaucidium* and *Coptis-Zanthorrhiza,* and one hundred and nine species of the Ranunculaceae have been examined cytologically. The material was obtained in the form of seeds which were planted and grown out of doors at The Blandy Experimental Farm. Seeds of twenty-two genera and four hundred and nine species were planted. Of these about one hundred and fifty species germinated. (Approximately forty "species" of *Aquilegia* received as seeds proved to be such a mixture of kinds, presumably through hybridization that they were not included in this study.) The survivors of those remaining and the few species received as plants will be entered into the permanent collections of The Blandy Experimental Farm. Some of the forms available were not examined by the writer.

Both mitotic and meiotic material has been employed in the cytological examinations. In the former case root tips were fixed in "Craf" fixative 10–12 hours and transferred after a momentary rinse in water to 70% alcohol where they were stored until needed. Stains employed in preparing the root tips were Newton's iodine-crystal violet, Heidenhain's haematoxylin, and Feulgen's nuclear stain. By far the most constant and satisfactory results were obtained with Feulgen's. Since the technique employed by the writer has not been widely used in cytological work a brief description will be included. Whole root tips were transferred directly from the 70% alcohol storage medium to the hydrolyzing fluid and

kept at 60 degrees C. for 15 minutes, rinsed in cold dilute hydrochloric acid, rinsed in water, and stained for two hours; they were then passed through three changes of SO_2 water and left in the last change 5 minutes, rinsed in water and transferred to 70% alcohol. From this stage onward the root tips were dehydrated, embedded and sectioned in the usual way. After the ribbon mount on the slide had dried sufficiently the paraffin was dissolved away with xylene and the balsam and cover-slip applied directly.

In the case of pollen mother cells temporary aceto-carmine mounts were made sometimes with and sometimes without prefixation in Carnoy's chloroform-alcohol-acetic or alcohol-acetic.

A Zeiss microscope was used and the drawings were made with a 1/12 inch oil immersion objective N.A. 1.25, an ×20 ocular and a camera lucida. This gave a magnification at bench level of 3560 diameters.

Chromosome Number and Type

The following list of chromosome numbers has been compiled from the literature, and and from the author's own work. The "type" of chromosomes where known is indicated on the basis of Langlet's (1932) work and that of the author. "Type" is indicated on a generic basis where no exceptions to type have occurred in any of the species of the genus observed by the writer or by Langlet. The arrangement of the genera is by tribes in the Engler sequence, that of the species within the genera primarily by chromosome number and secondarily in alphabetical order. The lists are therefore designed not only to compile the number and type of chromosomes known in the Ranunculaceae, but also to indicate the confusion of types within tribes, and to show the degree of polyploidy within each genus and thereby to see more easily the evidence for this or that basic number within the genera and ultimately in the family.

Unfortunately cytological investigators of plant groups frequently list the names of plants without giving the authorities for the names. In the following list of chromosome numbers in the Ranunculaceae a large proportion of the names taken from the literature carried no authority. The author's name has been supplied by the writer when the name under consideration occurred in the Index Kewensis and its supplements only once. In cases where the same name occurs several times with different authorities in Index Kewensis the authority has been omitted from the listed name and the several names from Index Kewensis placed directly below it with their synonyms as given in the Index. Where the authority for a name has been thus supplied by the writer the name is followed by an asterisk. A few of the older and more uncertain numbers reported in the literature have been omitted from this list.

A. Ovules on two sides of the ventral suture of the carpel, seldom single; fruit follicular, seldom a berry or capsule. Only *Callianthemum* with achenes.

Tribe I Hydrastideae: Flowers always single, without nectaries, calyx simple. Berry. Seed with strong outer integument far over-reaching the inner.

Genus: *Hydrastis* L. (1) N. America. Chromosome type uncertain. n-number = 13.

Name	n	$2n$	Author	Date
H. canadensis L.		26	Langlet	1928
H. canadensis L.		26	Francini	1931

Genus: *Glaucidium* Sieb. & Zucc. (2) Japan, China. Chromosome type uncertain. *n*-number = 10.

Name	*n*	2*n*	Author	Date
G. palmatum Sieb. & Zucc.		20	Miyaji	1927
G. palmatum Sieb. & Zucc.		20	Matsuura & Suto	1935

Engler and Gilg (1924) recognize the tribe Hydrastideae separated from Prantl's (1891) Paeonieae. Cytological as well as the morphological characteristics of the two groups justify this change. In *Glaucidium* the chromosome number 10 is not more incompatible with the base 5 in the Paeonieae (see below) than it is with 13 in *Hydrastis*. However the chromosomes of *Hydrastis* and *Glaucidium* are very similar in size whereas they do not resemble those of the Paeonieae. The type of chromosome is not indicated in this tribe, nor in the tribe Paeonieae below since both these groups are placed in the Ranunculaceae only with doubt. Some authors, for instance Lotsy (1911), take these groups out of the family entirely and place them in the Berberidaceae and Langlet in his systematic consideration of the family follows Lotsy in this regard. In the present paper under the section on phylogeny the position of both these groups is left as a questionable matter. In the writer's opinion this entire group of plants including many of the herbaceous Berberidaceae needs to be reconsidered very carefully not only in the manner that Kumazawa (1938) and Langlet (1928) have done but by a competent systematist with sufficient background in both cyto-genetics and morphology to evaluate the cytological as well as the morphological reasons for the classification of these plants.

Tribe II. Paeonieae: Flowers almost always single, without nectaries, with calyx and corolla. Wall of carpel leathery fleshy. Seed with strong outer integument far over-reaching the inner.

Genus: *Paeonia* L. (15) Temp. As., Eur. Medit., (2) W. N. Amer. Large Ranunculus-type? chromosomes. *n*-numbers 5, 10. Plate X, Figs. 106, 107, 108.

Name	*n*	2*n*	Author	Date
P. albiflora Pall.*	5		Langlet	1927
P. albiflora Pall.*		10	Miyaji	1927
P. albiflora Pall.*	5		Morinaga & Fukushima	?
P. albiflora Pall.	5		Hicks & Stebbins	1934
P. albiflora Pall.* var. *Agida*	5		Langlet	1927
P. albiflora Pall.* var. *Boule de Neige*	5		Langlet	1927
P. albiflora Pall.* var. *Etienne Denis*	5		Langlet	1927
P. albiflora Pall.* var. *Kasugana*		10	Langlet	1927
P. albiflora Pall.* var. *Nobilissima*	5		Langlet	1927
P. albiflora Pall.* var. *Potsii plena*	5		Langlet	1927
P. albiflora Pall.* var. *Prince Antoine d'Ahrenberg*	5		Langlet	1927
P. albiflora Pall.* var. *Rubens*	5		Langlet	1927

Name	*n*	2*n*	Author	Date
P. anomala L.*		10	Langlet	1927
P. anomala L.* *hybrida*	5		Langlet	1927
P. anomala L.* *nudicarpa*	5		Langlet	1927
P. anomala L.* × *tenuifolia* L.*		10	Langlet	1927
P. Beresowskyi Komarov *		10	Dark	1936
P. Broteri Boiss. & Reut.	5		Stebbins	1938
P. Brownii Dougl.	5		Stebbins	1938
P. Brownii Dougl.		10	Gregory	unpubl.
P. californica Nutt.	5		Stebbins & Ellerton	1939
P. Cambessedesii Willk.* (*P. corallina* Retz.)		10	Dark	1936
P. corallina Retz.* var. *Corsica*		10	Langlet	1927
P. corallina Retz.* *Russii*		10	Langlet	1927
P. corallina Retz.* *triternata*	5		Langlet	1927
P. Delavayi Franch.*		10	Dark	1936
P. Delavayi Franch.* *lutea*	5		Langlet	1927
P. Emodi Wall.* (*P. anomala* L.)		10	Dark	1936
P. Mlokasewitschii Lomak.*		10	Langlet	1927
P. Mlokasewitschii Lomak.	5		Hicks & Stebbins	1934
P. montana (author?)	5		Morinaga & Fukushima	?
P. moutan Sims *	5		Langlet	1927
P. obovata Maxim.*	5		Stebbins	1938
P. officinalis? (*P. officinalis* Falk = *anomala* L. *P. officinalis* Gouan = *peregrina* Mill *P. officinalis* Hayne = *paradoxa?* *P. officinalis* Pall. = *corallina* Retz. *P. officinalis* Thunb. = *moutan* Sims *P. officinalis* L.)		10	Dark	1936
P. peregrina? (*P. peregrina* Tenore = *paradoxa?* *P. peregrina* Mill.)		10	Dark	1936
P. suffruticosa Andr.	5		Sax	1932
P. suffruticosa Andr.	5		Hicks & Stebbins	1934
P. suffruticosa Andr. (*P. moutan* Sims)		10	Sax	1937
P. tenuifolia L.*		10	Langlet	1927
P. tenuifolia L.	5		Hicks & Stebbins	1934

Name	*n*	2*n*	Author	Date
P. tenuifolia L.*		10	Dark	1936
P. tenuifolia L.		10	Marquardt	1937
P. trollioides (author?)		10	Dark	1936
P. Veitchii Lynch *	5		Langlet	1927
P. Veitchii Lynch		10	Gregory	unpubl.
P. Bakeri (author?)		20	Langlet	1927
P. corallina Retz.	10		Stebbins	1938
P. coriacea Boiss.*	10		Langlet	1927
P. corsica Sieber * (*P. corallina* Retz.)	10		Stebbins	1938
P. decora Anders.*	10		Langlet	1927
P. obovata Maxim.* var. *alba*		20	Langlet	1927
P. officinalis L.(?)		20	Gregory	unpubl.
P. officinalis L.* var. *eufemina*	10		Langlet	1927
P. officinalis L.* var. *humilis*	10		Langlet	1927
P. officinalis L.* var. *leijocarpa*	10		Langlet	1927
P. officinalis L.* var. *mutabilis*	10		Langlet	1927
P. officinalis L.* var. *rubr. plen.*	10		Langlet	1927
P. officinalis L.* var. *villosa*	10		Langlet	1927
P. Smouthii Hybr.		20	Dark	1936
P. tenuifolia L.*		20	Dark	1936
P. tomentosa Stapf.	10		Stebbins	1938
P. Wittmaniana Hartwiss.*		20	Langlet	1927

Paeonia has proved to be one of the favorite objects for cytological study because of the large size and low number of its chromosomes. The works of Sax (1932), Hicks and Stebbins (1934), Dark (1936), Sax (1937), Sinoto (1938), Stebbins (1938), and Stebbins and Ellerton (1939) on the cyto-genetics and detailed behavior of the chromosomes at meiosis, as well as chromosome numbers, and especially Langlet (1927) on chromosome numbers give an exceptionally clear picture of the cytological situation in this genus. Polyploidy has evidently played very little part in the speciation of the genus whereas from some of the meiotic behavior (Sax 1937) structural rearrangements of the chromosomes may have exerted considerable influence. The taxonomic position of the genus is still somewhat obscure.

Tribe III. Helleboreae: Flowers single or several. Wall of carpel seldom fleshy. Outer integument of ovules not longer than the inner.

Genus: *Caltha* L. (16) Temp. N. and S. hemispheres. Large Ranunculus-type chromosomes. *n*-numbers = 16, 24, 28, 29?, 30, 32. Plate V Fig. 61.

Name	*n*	2*n*	Author	Date
C. laeta Schott * var. *alpina* (*C. palustris* L.)		32	Langlet	1927
C. palustris L.*		32	Langlet	1927
C. palustris L.		32	Lewitsky	1931

Name	*n*	2*n*	Author	Date
C. palustris L.*		32	Langlet	1932
C. palustris L.		32	Gregory	unpubl.
C. leptocephala?		48	Langlet	1927
C. leptocephala? var. *major*		48	Langlet	1932
C. radicans T. F. Forst.		48	Hocquette	1922
C. palustris L.* var.		56	Langlet	1927
C. palustris L.* var.		58	Langlet	1927
C. palustris L.* var.		60	Langlet	1932
C. palustris L.* var. *abisko*		56	Langlet	1936
C. palustris L.* *flor. plen.*		58–59	Langlet	1927
C. palustris L.* *flor. plen. nana*		58–59	Langlet	1927
C. palustris L.* *flor. plen. praecox*		58–59	Langlet	1927
C. palustris L. var. *semiplena*		58–59	Langlet	1927
C. polypetala Hochst.*		64	Langlet	1932
C. sp.		64	Langlet	1932

The genus *Caltha* which is ordinarily associated taxonomically with the succeeding genus *Trollius* differs from the latter in respect to number and stability of its chromosomes. The *n*-number 8 does not occur in the genus and although $n = 16$ in the "pure" species high polyploids are the rule. In varieties of species so many irregularities occur that only approximate numbers can be established and these do not fit in an 8-series of polyploids. Evidently polyploidy has played a prominent role toward speciation in this genus.

Genus: *Trollius* L. (12) N. Temp. Large Ranunculus-type chromosomes. *n*-numbers = 8, 16. Pl. XII, Fig. 132.

Name	*n*	2*n*	Author	Date
T. acaulis Lindl.*		16	Langlet	1932
T. acaulis Lindl.	8		Matsuura & Suto	1935
T. albiflorus?		16	Langlet	1932
T. asiaticus L.		16	Lewitsky	1931
T. asiaticus L.*		16	Langlet	1932
T. caucasicus Stev.*		16	Langlet	1927
T. chinensis Bunge* (*T. asiaticus* L.)		16	Langlet	1927
T. europaeus L.*		16	Langlet	1927
T. europaeus L.		16	Lewitsky	1931
T. europaeus L.	8		Matsuura & Suto	1935
T. giganteus Hort. (*T. europaeus* L.)		16	Langlet	1932
T. hybridus Hort. var. *Orange Globe*		16	Langlet	1927
T. japonicus Miq.* (*T. asiaticus* L.)		16	Lewitsky	1931

Name	*n*	2*n*	Author	Date
T. patulus?		16	Lewitsky	1931
(*T. patulus* Bieb. = *caucasicus* Stev. *T. patulus* Salisb.)				
T. purpuratus (author?)		16	Matsuura & Suto	1935
T. Riederianus Fisch. & Mey. (*T. patulus* Salisb.)		16	Sakai	1934
T. yunnanensis Ulbr.		16	Gregory	unpubl.
T. americanus Muhl.*		32	Langlet	1932

Only one tetraploid has been reported in this genus, all other species having the *n*-number = 8. As was pointed out above this is in sharp contrast to the situation in the closely related genus *Caltha*.

Genus: *Callianthemum* C. A. Mey. (3) Alp. and centr. As. Large Ranunculus-type chromosomes. *n*-numbers = 8, 16.

Name	*n*	2*n*	Author	Date
C. coriandraefolium Reichb.* (*C. rutaefolium* C. A. Mey.)		16	Langlet	1932
C. anemonoides? (*C. anemonoides* Endl. = *rutaefolium* Mey. *C. anemonoides* Kern = *Ranunculus anemonoides*? *C. anemonoides* Zahlb. = *Ranunculus anemonoides*?)		32	Langlet	1932
C. miyabeanum Tatewaki		32	Sakai	1935

The genus *Callianthemum* has been changed around considerably in regard to its taxonomic position. Here it is considered along with *Caltha* and *Trollius* in the Engler sequence. With these two genera it constitutes the subtribe Trolliinae of Lotsy (1911). Langlet (1932) associates it with *Adonis* and Kumazawa (1938) supports Langlet's position.

Genus: *Helleborus* L. (15) Medit. subalp. Large Ranunculus-type chromosomes. *n*-number = 16. Pl. VIII, Figs. 91, 92.

Name	*n*	2*n*	Author	Date
H. abschasicus A. Br.		32	Gregory	unpubl.
H. antiquorum A. Br.*		32	Langlet	1932
H. corsicus Willd.* (*H. lividus* Soland.)		32	Langlet	1932
H. dumetorum Waldst. & Kit.* (*H. viridis* L.)		32	Langlet	1932
H. foetidus L.	16		Mottier	1897

Name	*n*	2*n*	Author	Date
H. foetidus L.		32	Overton, J. B.	1905
H. foetidus L.*		32	Langlet	1927
H. foetidus L.		32	Lewitsky	1931
H. foetidus L.*	16		Pelletier	1936
H. foetidus L.		32	Gregory	unpubl.
H. hybridus Hort.		32	Langlet	1927
H. multifidus Vis.* (*H. viridis* L.)		32	Langlet	1932
H. niger L.*		32	Langlet	1927
H. odorus Waldst. & Kit.*		32	Langlet	1932
H. orientalis? (*H. orientalis* Gars. = *cyclophyllus* Boiss. *H. orientalis* Lam.)		32	Langlet	1932
H. viridis L.		32	Lewitsky	1931
H. viridis L.*		32	Langlet	1932

The genus *Helleborus*, although polyploid, is numerically the most stable genus in the family, only the *n*-number 16 being so far represented. Several earlier workers reported the number $n = 12$ but this is probably erroneous. Taxonomically this and the succeeding genus *Eranthis* form a natural group differing considerably from other members of the tribe Helleboreae.

Genus: *Eranthis* Salisb. (7) med. east As. Large Ranunculus-type chromosomes. *n*-number = 8. Pl. VIII, Fig. 90.

Name	*n*	2*n*	Author	Date
E. cilicica Schott & Kotschy *		16	Langlet	1932
E. hyemalis Salisb.*		16	Boecher	1932
E. hyemalis Salisb.*	8		Archambault	1937
E. hyemalis Salisb.		(48)	Gregory	unpubl.

This small genus constitutes with the genus *Helleborus* the subtribe Helleborinae of Lotsy (1911). It too is exceptionally stable numerically but differs from *Helleborus* in having the *n*-number 8 rather than 16. Included in the list of numbers above is the 2*n* count of 48 by the writer from a root tip in which all the cells were of the hexaploid constitution. The occurrence of highly polyploid individual cells in root tips of the Ranunculaceae is not uncommon and has been reported by Langlet (1927). The present number is reported to show that the stable genus *Eranthis* is no exception and that although polyploidy can occur somatically it has not resulted in the perpetuation of polyploid races. In most cases, individually polyploid cells observed by the writer in the Ranunculaceae occur in the large cells just back of the growing point of the root tips. No special study has been made as to whether the increase in cell size results in, or from the increase in number of chromosomes.

Genus: *Nigella* L. (16) medit. Large Ranunculus-type chromosomes. *n*-numbers = 6, 7. Pl. VIII, Fig. 94. Pl. IX, Figs. 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105.

Name	*n*	2*n*	Author	Date
N. aristata Sibth. & Sm.* (*N. arvensis* L.)		12	Langlet	1927
N. arvensis L.		12	Hocquette	1922
N. arvensis L.*	6		Langlet	1927
N. arvensis L.	6	12	Gregory	unpubl.
N. damascena L.*	6		Langlet	1927
N. damascena L.		12	Lewitsky	1931
N. damascena L.	6	12	Gregory	unpubl.
N. damascena L.* var. *flor. plen.* Miss Jekyll		12	Langlet	1927
N. damascena L. var. *flor. plen.* Miss Jekyll		12	Gregory	unpubl.
N. damascena L. var. *genuina* Briq.		12	Hocquette	1922
N. garidella Spenn.*		12	Langlet	1927
N. garidella Spenn.		12	Lewitsky	1931
N. hispanica L.*	6		Langlet	1927
N. hispanica L.		12	Lewitsky	1931
N. hispanica L.	6	12	Gregory	unpubl.
N. nigellastrum Willk. (*N. garidella* Spenn.)		12	Hocquette	1922
N. nigellastrum Willk. (*N. garidella* Spenn.)	6		Gregory	unpubl.
N. orientalis L.*	6		Langlet	1927
N. orientalis L.		12	Lewitsky	1931
N. orientalis L.	6	12	Gregory	unpubl.
N. sativa L.		12	Hocquette	1922
N. sativa L.*	6		Langlet	1927
N. sativa L.		12	Lewitsky	1931
N. sativa L.	6	12	Gregory	unpubl.
N. viridis (author?)		12	Franck	1911
N. diversifolia Franch.		14	Lewitsky	1931
N. diversifolia Franch.*		14	Langlet	1932

With the exception of the species *N. diversifolia* with $n = 7$, all the species of *Nigella* have $n = 6$. No polyploidy is known in the genus. The *n*-number 7 appears to be very unusual here and to the casual observer might seem to bear the same relation to the 8-series of the family as do the 7-chromosome members of *Anemone* and *Ranunculus*. From an examination of the idiograms of *N. diversifolia* and other species of *Nigella* in Lewitsky's (1931) paper, it is entirely conceivable that this number arose from a reduplication of one of the pairs of chromosomes in the 6-chromosome species. In the writer's diagrammatic representation of the phylogenetic relations in the family (see phylogenetic chart II), *Nigella* is shown to be derived from an 8-chromosome ancestor but *N. diversifolia* probably does not represent an intermediate step in the process of that evolution.

Genus: *Isopyrum* L. (27) mostly Asian. Small Thalictrum-type chromosomes. *n*-number = 7, Pl. VIII, Fig. 89.

Name	*n*	2*n*	Author	Date
I. biternatum Torr. & Gray		14	Sorokin	1929
I. fumarioides L.*		14	Langlet	1927
I. fumarioides L.		14	Lewitsky	1931
I. fumarioides L.		14	Gregory	unpubl.

In the Engler sequence this genus is removed somewhat from its closest relative *Aquilegia* in the Helleboreae. Lotsy (1911) includes it with *Aquilegia* and *Leptopyrum* (which is synonymous with *Isopyrum*) in the subtribe Isopyrinae. The inclusion of this genus in the Helleboreae is one of the noteworthy cases where the two types of chromosomes in the Ranunculaceae have been placed together taxonomically.

Genus: *Coptis* Salisb. (11) subarctic. Small Thalictrum-type? chromosomes. *n*-number = 9.

Name	*n*	2*n*	Author	Date
C. japonica Makino * (*C. orientalis* Maxim.)		18	Langlet	1932
C. japonica Makino (*C. orientalis* Maxim.)	9		Akemine	1935
C. japonica Makino (*C. orientalis* Maxim.)	9		Matsuura & Suto	1935
C. trifoliata Makino *		18	Langlet	1932
C. trifoliata Makino		18	Nakajima	1933

Genus: *Zanthorrhiza* L'Her. (1) East. N. Amer. Small Thalictrum-type? chromosomes. *n*-number = 18.

Name	*n*	2*n*	Author	Date
Z. apiifolia L'Her.*		36	Langlet	1932

This and the preceding genus form such a distinct unit both taxonomically and cytologically in chromosome type and number that they are here discussed together. Lotsy (1911) groups these two genera as a sub-unit in the subtribe Cimicifuginae along with *Cimicifuga* and *Actaea*. Since the divergence from the rest of the family is so marked the writer has given these genera equal tribal rank with the Helleboreae etc.

Genus: *Actaea* L. (13 including Cimicifuga) N. Hem. Large Ranunculus-type chromosomes. *n*-number = 8, Pl. I, Fig. 6.

Name	*n*	2*n*	Author	Date
A. alba Mill.*		16	Langlet	1932
A. alba Mill.		16	Gregory	unpubl.
A. erythrocarpa Fisch.* (*A. spicata* L.)		16	Lewitsky	1931
A. rubra Willd.*		16	Langlet	1932
A. spicata L.*		16	Langlet	1927

Genus: *Cimicifuga* L. (13 including *Actaea*) N. Hem. Large Ranunculus-type chromosomes. *n*-number = 8. Pl. VI, Figs. 63, 64, 65.

Name	*n*	2*n*	Author	Date
C. acerina Tanaka *	8		Sugiura	1937
C. americana?		16	Langlet	1932
(*C. americana* Muhl. = *cordifolia* Pursh *C. americana* Michx.)				
C. cimicifuga (author?)		16	Langlet	1927
C. cordifolia Pursh *		16	Langlet	1932
C. dahurica?		16	Langlet	1932
(*C. dahurica* Huth = *Actinospora dahurica* Turcz. (*C. dahurica* Maxim.)				
C. foetida L.		16	Lewitsky	1931
C. japonica Spreng.*		16	Langlet	1932
C. racemosa Nutt.	8	16	Gregory	unpubl.
C. simplex Wormsk.* (*C. foetida* L.)		16	Langlet	1932

Genus: *Anemonopsis* Sieb. & Zucc. (1) Japan. Large Ranunculus-type chromosomes. *n*-number = 8.

Name	*n*	2*n*	Author	Date
A. macrophylla Sieb. & Zucc.*		16	Langlet	1932

Cimicifuga together with *Actaea* forms a close taxonomic unit and should not, on the basis of cytology or general morphology, be confused with *Coptis* and *Zanthorrhiza*. Its chromosome numbers are stably diploid. The genus *Anemonopsis* has not been observed by the writer and is included here according to the classification of Lotsy.

Genus: *Aquilegia* L. (50) N. Hemisphere. Small Thalictrum-type chromosomes. *n*-numbers = 7, 14. Pl. III, Figs. 19 to 39 incl.

Name	*n*	2*n*	Author	Date
A. akitensis Huth		14	Sakai	1935
A. alpina L.		14	Lewitsky	1931
A. alpina L.		14	Gregory	unpubl.
A. atropurpurea?		14	Langlet	1927
(*A. atropurpurea* Miq. = *Buergeriana* Sieb. & Zucc. *A. atropurpurea* Willd. = *viridiflora* Pall.)				
A. baikalensis (author?)		14	Gregory	unpubl.
A. caerulea James *	7		Winge	1925

Name	*n*	2*n*	Author	Date
A. canadensis L.*	7		Winge	1925
A. canadensis L.	7	14	Gregory	unpubl.
A. chrysantha Gray	7	14	Skalinska	1928
A. chrysantha Gray		14	Gregory	unpubl.
A. coccinea Small	7		Gregory	unpubl.
A. dichroa Freyn		14	Gregory	unpubl.
A. einseleana Fr. Schultz		14	Gregory	unpubl.
A. flabellata Sieb. & Zucc.*	7		Skalinska	1931
A. flabellata Hort.		14	Anderson & Schafer	1931
A. flabellata Sieb. & Zucc.*		14	Skalinska	1935
A. glandulosa Fisch.		14	Gregory	unpubl.
A. haylodgensis Hort.		14	Langlet	1927
A. jucunda?		14	Gregory	unpubl.
(*A. jucunda* Fisch. & Lal. = *glandulosa* Fisch. *A. jucunda* Fisch. = *vulgaris* L.)				
A. longissima Gray	7	14	Gregory	unpubl.
A. nigricans Baumg.* (*A. vulgaris* L.)	7		Winge	1925
A. skinneri Hook.	7		Gregory	unpubl.
A. truncata Fisch. & Mey.* (*A. formosa* Fisch.)	7		Skalinska	1931
A. vulgaris L.*	7		Winge	1925
A. vulgaris L.		14	Lewitsky	1931
A. vulgaris L.	7		Gregory	unpubl.
A. hirsutissima Timb.		28	Gregory	unpubl.

Aquilegia has been the object of considerable genetic study from the standpoint of interspecific crosses. This genus is one of the most remarkable groups among the angiosperms for its interfertility. Polyploidy is exceptionally rare and the diploid interspecific hybrids show very little sterility. This fact becomes even more remarkable when it is noted that the high interfertility is just as common between species on opposite sides of the earth as between geographically related species. This situation is in great contrast to the condition in *Nigella* which occupies only a limited region of the earth with a very few species where intersterility is the rule (Gregory unpubl.). It should be emphasized that these two genera form very distinct and natural units.

Genus: *Delphinium* L. (200) N. Hemisphere. Large Ranunculus-type chromosomes. *n*-numbers = 8, (12)?, 16, 24. Pl. VI, VII, VIII, Figs. 66 to 88 incl.

Name	*n*	2*n*	Author	Date
D. ajacis L.	8	16	Tjebbes	1927
D. ajacis L.*		16	Langlet	1927
D. ajacis L.		16	Lewitsky	1931

Name	*n*	2*n*	Author	Date
D. ajacis L.		16	Gregory	unpubl.
D. brachycentrum Ledeb.*		16	Langlet	1932
D. Brunonianum Royle		16	Lewitsky	1931
D. cardiopetalum DC.	8		Tjebbes	1927
D. cardiopetalum DC. (*D. halteratum* Sibth. & Sm.)		16	Lewitsky	1931
D. chinense Fisch.* (*D. grandiflorum* L.)		16	Langlet	1927
D. consolida L.		16	Hocquette	1922
D. consolida L.	8		Tjebbes	1927
D. consolida L.*		16	Langlet	1927
D. consolida L.		16	Lewitsky	1931
D. consolida L.	8	16	Gregory	unpubl.
D. Delavayi Franch.		16	Lewitsky	1931
D. gayanum Wilmott		16	Gregory	unpubl.
D. grandiflorum L.	8	(32)	Gregory	unpubl.
D. nudicaule Torr. & Gray *	8		Tjebbes	1927
D. nudicaule Torr. & Gray *		16	Lawrence	1936
D. orientale var.?	ca. 8		Beckman	1928
D. orientale? (*D. orientale* Losc. = *Loscosii* Costa *D. orientale* J. Gay)		16	Gregory	unpubl.
D. penardi Huth	8		Gregory	unpubl.
D. peregrinum L.	8		Gregory	unpubl.
D. pictum Willd. (*D. Requienii* DC.)		16	Gregory	unpubl.
D. scopulorum Gray	8	16	Gregory	unpubl.
D. speciosum? (*D. speciosum* Janka = *elatum* L. *D. speciosum* Bieb.)		16	Langlet	1927
D. staphysagria L.		16	Hocquette	1922
D. tatsiense Franch.		16	Lewitsky	1931
D. tricorne Michx.	8		Gregory	unpubl.
D. yunnanense Franch.	8	(32)	Gregory	unpubl.
D. Moerheimii (Hybrid)		24	Lawrence	1936
D. azureum Michx.		32	Lewitsky	1931
D. bulleyanum Forrest		32	Gregory	unpubl.
D. carolinianum Walt. (*D. azureum* Michx.)		32	Gregory	unpubl.
D. caucasicum C. A. Mey.		32	Gregory	unpubl.
D. Duhmbergii Huth		32	Gregory	unpubl.
D. elatum L.		32	Lewitsky	1931

Name	*n*	2*n*	Author	Date
D. elatum L.		32	Gregory	unpubl.
D. fissum Waldst. & Kit.		32	Hocquette	1922
D. flexuosum Raf.		32	Gregory	unpubl.
D. formosum Boiss. & Huet		32	Gregory	unpubl.
D. hybridum? (*D. hybridum* L. = *elatum* L. *D. hybridum* Steph.)		32	Langlet	1927
D. Ruysii (Hybrid)		32	Lawrence	1936
D. staphysagria L.*		32	Langlet	1927
D. staphysagria L.		32	Lewitsky	1931
D. truncatum (author?)		32	Langlet	1927
D. belladonna (hort)		48	Langlet	1927
D. Lamartini (Hybrid)		48	Lawrence	1936

The genus *Delphinium* together with *Aconitum* represents the highest development of floral morphology in the family Ranunculaceae. Not only is zygomorphy here introduced into the family but the floral organs, exclusive of the stamens, approach definite rather than indefinite numbers. Cytologically this genus has been studied very little compared to the number of species in the genus.

Polyploidy has evidently played an important role in the speciation of the genus and within certain sections interspecific hybridization must also have had some effect. Lawrence (1936) describes the origin of fertile belladonna hybrids and attributes the acquired fertility of this hexaploid to amphidiploidy. *D. Lamartini* is a belladonna type which is hexaploid. *D. Ruysii* is a tetraploid which arose in 1929 *D. nudicaule* ($n = 8$) seedlings and is believed because of its tendency to throw red flowers to be a hybrid between diploid *D. nudicaule* and tetraploid *D. elatum*. Lawrence suggested that an unreduced *D. nudicaule* gamete was fertilized by a normal *D. elatum* gamete thus giving rise to the tetraploid *D. Ruysii*.

Genus: *Aconitum* L. (60) N. Hemisphere. Large Ranunculus-type chromosomes. *n*-numbers = 8, (12)?, 16, 24, 32, 48. Pl. I, Figs. 1 to 5 incl.

Name	*n*	2*n*	Author	Date
A. barbatum Patr. (*A. Lycoctonum* L.)		16	Darlington	1932
A. excelsum? (*A. excelsum* Turcz. = *Lycoctonum* L. *A. excelsum* Reichb.)		16	Langlet	1927
A. Forrestii Stapf.		16	Schafer & La Cour	1934
A. Hemsleyanum Pritz.		16	Schafer & La Cour	1934
A. heterophyllum Wall.		16	Schafer & La Cour	1934
A. luridum Hook. f. & Thoms.		16	Afifi	1933
A. luridum Hook. f. & Thoms.		16	Schafer & La Cour	1934

Name	*n*	2*n*	Author	Date
A. Lycoctonum L.		16	Lewitsky	1931
A. Lycoctonum L.		16	Afifi	1933
A. Lycoctonum L.		16	Schafer & La Cour	1934
A. orientale Mill.		16	Lewitsky	1931
A. orientale Mill.		16	Afifi	1933
A. orientale Mill.		16	Schafer & La Cour	1934
A. paniculatum Lam.*		16	Schafer & La Cour	1934
A. reclinatum Gray	8	16	Gregory	unpubl.
A. septentrionale Koelle * (*A. Lycoctonum* L.)		16	Langlet	1927
A. thyriacum Blocki		16	Schafer & La Cour	1934
A. Toppinii Stapf.		16	Schafer & La Cour	1934
A. transsectum Diels		16	Schafer & La Cour	1934
A. uncinatum L.	8	16	Gregory	unpubl.
A. umbrosum Kom.		16	Sakai	1933
A. variegatum? (*A. variegatum* Hook. f. & Thoms. = *uncinatum* L. *A. variegatum* L.)		16	Schafer & La Cour	1934
A. volubile? (*A. volubile* Moench = *variegatum* L. *A. volubile* Muhl. = *uncinatum* L. *A. volubile* Koelle *A. volubile* Pall.)		16	Langlet	1932
A. vulparia Rchb.*		16	Langlet	1927
A. vulparia Rchb.		16	Darlington	1932
A. vulparia Rchb.		16	Schafer & La Cour	1934
A. yuparense Takeda		16	Sakai	1934
A. Sparks Var.		24	Langlet	1927
A. anglicum Stapf.		32	Darlington	1932
A. anthora L.		32	Lewitsky	1931
A. anthora L.		32	Schafer & La Cour	1934
A. californicum (author?)		32	Langlet	1927
A. Delavayi Franch.*		32	Langlet	1927
A. Fischeri Rchb.		32	Sakai	1933
A. Kusnezoffii Rchb.*		32	Langlet	1927
A. Kusnezoffii Rchb.*		32	Sakai	1933
A. napellus L.		32	Lewitsky	1931
A. napellus L.*		32	Langlet	1932
A. napellus L.		32	Darlington	1932
A. napellus L.		32	Schafer & La Cour	1934
A. napellus L.		32	Gregory	unpubl.

Name	*n*	2*n*	Author	Date
A. paniculatum Lam.*		32	Langlet	1927
A. sachalinense Fr. Schm.		32	Sakai	1933
A.? spicatum Donn (*A. napellus* L.)		32	Schafer & La Cour	1934
A. subcuneatum Nakai		32	Sakai	1933
A. Stoerkianum (author?)		32–34	Schafer & La Cour	1934
A. volubile Pall.		32	Darlington	1932
A. volubile Pall.		32	Schafer & La Cour	1934
A. yezoense Nakai		32	Sakai	1933
A. palmatum D. Don *		45–47	Schafer & La Cour	1934
A.? palmatum D. Don *		48	Schafer & La Cour	1934
A. Wilsonii Stapf.*		ca. 64	Langlet	1927
A. Wilsonii Stapf.		64	Schafer & La Cour	1934
A. sp.		96	Schafer & La Cour	1934

Schafer and La Cour (1934) treated this genus from a strictly cyto-taxonomic standpoint and showed that by means of karyotype analysis the two main sections of the genus could be distinguished. All of the members of the section Lycoctonum examined had $n = 8$, section Anthora, with one species examined $n = 16$, and section Euaconitum, with 14 species examined, $n = 8, 12, 16, 24, 32$, and 48. The Euaconites could be distinguished as a group chiefly by chromosome size and morphology.

B. Ovules single at the base of the ventral suture, often still rudimentary along the sides of the same. Achenes single-seeded.

Tribe IV. Anemoneae: Flowers single or in cymose or racemose inflorescences. Fruit a single-seeded achene.

Genus: *Anemone* L. (90) Temp. N. and S. Hemispheres. Large Ranunculus-type chromosomes. *n*-numbers = 7, 8, 12, 14, 16, 24. Pl. II, Figs. 9 to 13, and 15 to 18.

Name	*n*	2*n*	Author	Date
A. acutiloba Laws.*		14	Langlet	1932
A. debilis Fisch.	7		Sakai	1935
A. demissa Hook. f. & Thoms.* var. *umbellata*	7		Langlet	1936
A. flaccida Fr. Schmidt	7		Matsuura & Suto	1935
A. hepatica L.		14	Moffett	1932
A. hepatica L.		14	Boecher	1932
A. hepatica L.		14	Nakajima	1933
A. hepatica L.		14	Matsuura & Suto	1935
A. hepatica L.		14	Pop	1937
A. hepatica L.		14	Gregory	unpubl.
A. heptica L.* var. *alb. ros.*		14	Langlet	1927
A. hepatica L. var. *candida*		14	Langlet	1927
A. hepatica L. var. *laevigata*		14	Nakajima	1933
A. hepatica L.* var. *rubr. plen.*		14	Langlet	1927

Name	*n*	2*n*	Author	Date
A. narcissiflora?	7–8		Langlet	1927
A. narcissiflora L.		14	Sakai	1934
A. narcissiflora?		14	Langlet	1936
(*A. narcissiflora* Hook. & Arn. = *multifida* Poir.)				
A. albana Stev.*		16	Langlet	1932
A. alpina?		16	Rosenthal	1936
(*A. alpina* Scop. = *baldensis* L. *A. alpina* L.)				
A. altaica Fisch.*		16	Guinochet	1935
A. apennina L.		16	Boecher	1932
A. baicalensis Turcz.*	8		Langlet	1927
A. blanda Schott & Kotschy*		16	Langlet	1927
A. borealis Richards (*A. parviflora* Michx.)	8		Moffett	1932
A. bulgarica Velen.		16	Rosenthal	1936
A. caroliniana Walt. (*A. decapetala* Arduini)	8		Moffett	1932
A. cernua Thunb.		16	Nakajima	1931
A. cernua Thunb.		16	Matsuura & Suto	1935
A. coronaria L.		16	Nakajima	1931
A. coronaria L.*	8		Guinochet	1935
A. coronaria L.	8		Dahl	1937
A. cylindrica Gray	8		Guinochet	1935
A. cylindrica Gray	8		Dahl	1937
A. cylindrica Gray	8		Gregory	unpubl.
A. dichotoma L.*		16	Guinochet	1935
A. fulgens J. Gay		16	Moffett	1932
A. fulgens J. Gay		16	Nakajima	1936
A. georgica (author?)		16	Langlet	1932
A. hepatica L.* var. *acuta*		16	Sugiura	1931
A. hortensis?	8		Guinochet	1935
A. hortensis L.	8		Nakajima	1936
(*A. hortensis* Thore = *fulgens* J. Gay *A. hortensis* L.)				
A. hupehensis Hort. (*A. japonica* Sieb. & Zucc. var. *hupehensis*)		16	Langlet	1927
A. japonica Sieb. & Zucc.	8		Takamine	1916
A. japonica Sieb. & Zucc.	8		Nakajima	1931
A. japonica Sieb. & Zucc.	8		Moffett	1932
A. japonica Sieb. & Zucc.		16	Matsuura & Suto	1935

Name	*n*	2*n*	Author	Date
A. japonica Sieb. & Zucc.	8		Gregory	unpubl.
A. Leveillei Ulbr.*		16	Langlet	1932
A. Leveillei Ulbr.		16	Gregory	unpubl.
A. mexicana H. B. & K.	8		Moffett	1932
A. montana Hoppe *		16	Langlet	1927
A. montana Hoppe *		16	Zimmerman	1932
A. montana Hoppe		16	Rosenthal	1936
A. parviflora Michx.*	8		Langlet	1932
A. parviflora Michx.	8		Moffett	1932
A. patens L.		16	Rosenthal	1936
A. pavoniana Boiss.*		16	Langlet	1932
A. pratensis?		16	Langlet	1927
A. pratensis?		16	Boecher	1932
A. pratensis?		16	Zimmerman	1932
A. pratensis L.		16	Rosenthal	1936
(*A. pratensis* C. Koch = *montana* Hoppe *A. pratensis* Pall. = *sylvestris* L. *A. pratensis* Sibth. = *pulsatilla* L. *A. pratensis* L.)				
A. reflexa?		16	Rosenthal	1936
(*A. reflexa* Ledeb. = *caerulea* DC. *A. reflexa* Steph.)				
A. riparia Fernald	8		Dahl	1937
A. rivularis?		16	Langlet	1932
A. rivularis?		16	Guinochet	1935
(*A. rivularis* Wall. = *elongata* D. Don *A. rivularis* Buch.-Ham)				
A. rivularis Buch.-Ham var. *barbulata*		16	Gregory	unpubl.
A. sibirica L.	8		Moffett	1932
A. sylvestris L.	8		Moffett	1932
A. sylvestris L.*		16	Langlet	1927
A. sylvestris L.* var. *flor. plen.*		16	Langlet	1927
A. transsylvanica Heuff.		16	Pop	1937
A. vernalis L.		16	Moffett	1932
A. vernalis L.		16	Boecher	1932
A. virginiana L.*		16	Langlet	1932
A. virginiana L.	8		Dahl	1937
A. virginiana L.	8		Gregory	unpubl.

Name	*n*	2*n*	Author	Date
A. vitifolia Buch.-Ham.*		16	Langlet	1932
A. vitifolia Buch.-Ham.		16	Moffett	1932
A. baldensis?	12		Moffett	1932
(*A. baldensis* G. Don = *multifida* Poir. *A. baldensis* Lam. = *alpina* L. *A. baldensis* L.)				
A. decapetala Arduini	12		Moffett	1932
A. narcissiflora?	12		Winge	1917
A. nemorosa?		24	Guinochet	1935
(*A. nemorosa* Schang. = *altaica* Fisch. *A. nemorosa* L.)				
A. angulosa Lam.*	14		Langlet	1932
A. hepatica L.* var. *multiloba*		28	Langlet	1927
A. angulosa Lam. (*A. transsylvanica*?)		32	Rosenthal	1936
A. armena Boiss.*		32	Langlet	1932
A. blanda rosea Schott & Kotschy		32	Moffett	1932
A. Bogenhardiana Pritz.*	16		Zimmerman	1932
A. fulgens J. Gay *	16		Langlet	1932
A. Halleri All.		32	Rosenthal	1936
A. magellanica Hort.		32	Moffett	1932
A. multifida Poir		32	Langlet	1927
A. multifida Poir	16		Moffett	1932
A. multifida Poir *	16		Langlet	1932
A. nemorosa?		32	Moffett	1932
A. palmata L.*		32	Langlet	1932
A. pulsatilla Zinn.?	16		Moffett	1932
A. pulsatilla L.		32	Sakai	1935
A. pulsatilla L.		32	Rosenthal	1936
A. pulsatilla L.		32	Gregory	unpubl.
A. ranunculoides L.*	16		Langlet	1932
A. ranunculoides L.	16		Boecher	1932
A. rubra Lam. (*A. pulsatilla* L.)		32	Rosenthal	1936
A. rupicola Camb.*		32	Langlet	1927
A. rupicola Camb.		32	Moffett	1932
A. sylvestris L.		32	Gregory	unpubl.
A. trifolia?		32–30	Langlet	1932
(*A. trifolia* DC. = *reflexa* Steph. *A. trifolia* L.)				

Name	*n*	2*n*	Author	Date
A. vulgaris (author?)	16		Boecher	1932
A. montana Hoppe * var.	24	48	Moffett	1932

The genus *Anemone* characterizes the tribe Anemoneae which includes all those ranunculaceous species with achenes except *Callianthemum*. Although it is only the fourth largest genus in the family considerable cytological work has been done, especially by Moffett (1932). Polyploidy has evidently played a considerable part in the speciation of the genus and within the genus a 7-aneuploid series has become established. One tetraploid has been reported for this 7*n* group. There is no reason to suppose that this 7-chromosome group was not derived directly from some 8-chromosome ancestor.

Genus: *Knowltonia* Salisb. (6) S. Afr. Large Ranunculus-type chromosomes. *n*-number = 24.

Name	*n*	2*n*	Author	Date
K. vesicatoria Sims *		48	Langlet	1932

Knowltonia is sometimes included with the genus *Anemone*, but is here considered distinct.

Genus: *Anemonella* Spach. (1) N. Amer. Small Thalictrum-type chromosomes. *n*-number = 7. Pl. II, Fig. 14.

Name	*n*	2*n*	Author	Date
A. thalictroides (L.) Spach.		14	Sorokin	1929
A. thalictroides (L.) Spach.		14	Gregory	unpubl.

Anemonella is frequently given in synonymy with the genus *Anemone*. Lotsy includes it with *Thalictrum* in the subtribe Anemoninae. Its affinity with *Thalictrum* is not to be disputed but the cytological evidence as well as the general vegetative characteristics of the genus make its taxonomical relations with *Anemone* untenable.

Genus: *Clematis* L. (170) World wide. Large Ranunculus-type chromosomes. *n*-numbers = 8, 16, 24. Pls. IV and V, Figs. 40 to 60, and 62.

Name	*n*	2*n*	Author	Date
C. addisonii Britton	8		Gregory	unpubl.
C. alpina Mill		16	Sakai	1935
C. alpina Mill		16	Meurman & Therman	1939
C. alpina Mill		16	Gregory	unpubl.
C. Baron Veillard Hort.		16	Gregory	unpubl.
C. brevicaudata DC.		16	Gregory	unpubl.
C. campaniflora Brot.		16	Meurman & Therman	1939
C. crispa L.		16	Gregory	unpubl.
C. dioica?		16	Gregory	unpubl.
C. douglassii Hook.		16	Gregory	unpubl.
C. eriostemon Decne		16	Meurman & Therman	1939
C. flammula L.		16	Meurman & Therman	1939

Name	*n*	2*n*	Author	Date
C. Fremontii S. Wats.		16	Gregory	unpubl.
C. fusca Turcz.		16	Meurman & Therman	1939
C. globosa Royle (*C. orientalis* L.)		16	Gregory	unpubl.
C. heracleaefolia DC.		16	Nakajima	1933
C. heracleaefolia DC.	8		Nakajima	1937
C. heracleaefolia DC.		16	Gregory	unpubl.
C. heracleaefolia DC. var. *davidiana*	8		Gregory	unpubl.
C. hybrida Hort.		16	Meurman & Therman	1939
C. integrifolia L.		16	Meurman & Therman	1939
C. integrifolia L.		16	Gregory	unpubl.
C. Jackmanni Hybrid		16	Langlet	1927
C. Jackmanni Hybrid	8		Polinkova	1936
C. Jackmanni Hybrid		16	Meurman & Therman	1939
C. koreana Komar.		16	Meurman & Therman	1939
C. lasiantha Nutt.		16	Meurman & Therman	1939
C. ligusticifolia Nutt.		16	Meurman & Therman	1939
C. ligusticifolia Nutt.		16	Gregory	unpubl.
C. montana Wilsonii Sprague		16	Meurman & Therman	1939
C. montana rubens Ktze.		16	Meurman & Therman	1939
C. ochotensis Poir *		16	Langlet	1927
C. ochroleuca Ait.		16	Gregory	unpubl.
C. paniculata Thunb.		16	Langlet	1927
C. paniculata Thunb.		16	Gregory	unpubl.
C. Prins Hendrik Hort.		16	Meurman & Therman	1939
C. recta L.		16	Guignard	1885
C. recta L.*		16	Langlet	1927
C. recta L.		16	Meurman & Therman	1939
C. scottii Porter		16	Gregory	unpubl.
C. serratifolia Rehd.		16	Meurman & Therman	1939
C. stans Sieb. & Zucc.*		16	Langlet	1927
C. tangutica Korsh		16	Meurman & Therman	1939
C. tangutica Korsh	8	16	Gregory	unpubl.
C. texensis Buckl.		16	Meurman & Therman	1939
C. texensis Buckl.		16	Gregory	unpubl.
C. The President Hort.		16	Meurman & Therman	1939
C. Ville de Lyon Hort.		16	Meurman & Therman	1939
C. Ville de Lyon Hort.		16	Gregory	unpubl.
C. virginiana L.	8		Lindsay	1929
C. virginiana L.	8		Gregory	unpubl.
C. vitalba L.		16	Meurman & Therman	1939
C. viticella L.		16	Meurman & Therman	1939

Name	*n*	2*n*	Author	Date
C. mandschurica Rupr. (*C. recta* L.)		32	Meurman & Therman	1939
C. paniculata Thunb.		48	Meurman & Therman	1939
C. paniculata Thunb.	(32)		Gregory	unpubl.

The genus *Clematis* is the third largest genus of the family Ranunculaceae and with the possible exception of *Caltha* has the widest geographical range of any genus in the family. It has long been an important horticultural group of plants and some notable hybrid types are now widely cultivated. The genus represents the maximum development of the woody type in the family and possesses both deciduous and evergreen species.

In spite of its widespread geographic range, its prominence in horticultural circles and its exceptionally large and numerically low chromosomes, little cytological work had been done on the genus until Meurman and Therman (1939) and the writer made their contributions. Polyploidy scarcely exists in the genus, only two polyploid species having been reported. This is very interesting in the light of the evidence brought forward by Senn (1938) that woody plants of the Leguminosae are generally higher polyploids than the herbaceous types. Furthermore from a study of annual, perennial, and woody types in the Ranunculaceae and the method of origin of perennial and finally woody types by changes in the levels above ground of the so-called renewal buds it is indicated that the direction of evolution in this family has been from annual herbaceous to perennial herbaceous to perennial woody. Although the direction of evolution here is the same in this particular as that suggested by Senn for the Leguminosae polyploidy apparently had no causal relation.

Genus: *Myosurus* L. (7) Temp. Large Ranunculus-type chromosomes. *n*-number = 8.

Name	*n*	2*n*	Author	Date
M. minimus L.	8		Mann, G.	1892
M. minimus L.		16	Hocquette	1922

Genus: *Trautvetteria* Fisch. and Mey. (2) N. Amer. E. Asia. *n*-number = 8.

Name	*n*	2*n*	Author	Date
T. carolinensis Britton *		16	Langlet	1932
T. carolinensis Vail		16	Meyer	1937
T. japonica Sieb. & Zucc. (*T. palmata* Fisch & Mey.)	8		Matsuura & Suto	1935
T. palmata Fisch & Mey.*		16	Langlet	1932

Genus: *Ranunculus* L. (250) Mostly N. Hem. Large Ranunculus-type chromosomes. *n*-numbers = 7, 8, 14, 16, 21, 24, 28, 32, 40, 48, 64. Pl. XI, Figs. 109 to 123.

Name	*n*	2*n*	Author	Date
R. acer L.*	7		Langlet	1932
R. acer L.	7		Larter	1932
R. acer L.	7		Matsuura & Suto	1935
R. acer L.	7		Marsden-Jones & Turrill	1935

Name	*n*	2*n*	Author	Date
R. acer L.	7		Sakai	1935
R. acer L.		14	Boecher	1938
R. aconitifolius L.		14	Gregory	unpubl.
R. acris L.		12	Sorokin	1924
R. acris L.	7	14	Sorokin	1927
R. acris L.*		14	Langlet	1927
R. acris L.	7	14	Senjaninova	1926
R. acris L.		29–32	Senjaninova	1926
R. acris L.	7		Whyte	1929
R. acris L.		14	Gregory	unpubl.
R. acris L. (gynodimorphic race)		13–15	Sorokin	1924
R. acris L. (gynodimorphic race)		18	Sorokin	1924
R. acris L. (n 18 × n 12)		12	Sorokin	1927
R. acris L. (n 18 × n 12)		13	Sorokin	1927
R. acris L. (n 18 × n 12)		15	Sorokin	1927
R. acris L. (n 18 × n 12)		17	Sorokin	1927
R. acris L.* *flor. plen.*		14	Langlet	1927
R. acris L.* *femina*	7	14	Langlet	1927
R. acris L.* *stevenii*		14	Langlet	1927
R. aduncus Gren. & Godr.* (*R. Villarsii* DC.)		14	Langlet	1936
R. armeniacus?		14	Gregory	unpubl.
R. bulbosus L.	7		Matsuura & Suto	1935
R. carpaticus? (*R. carpaticus* Herbich = *montanus* Willd. *R. carpaticus* Wahlenb. = *thora* L.)		14	Langlet	1927
R. cassius Boiss.		14	Gregory	unpubl.
R. chius DC.		14	Sorokin	1929
R. chius DC.*		14	Langlet	1932
R. chius DC.		14	Larter	1932
R. constantinopalitanus? (*R. constantinopalitanus* Bory & Chaub. = *velutinus* Tenore *R. constantinopalitanus* Schur = *acris* L. *R. constantinopalitanus* Stev. = *palustris* L. *R. constantinopalitanus* Urv.)		14	Langlet	1936
R. Friesianus Jord.* (*R. acris* L.)		14	Langlet	1936

Name	*n*	2*n*	Author	Date
R. garganicus Tenore* (*R. millefoliatus* Vahl)		14	Langlet	1936
R. lacerus? (*R. lacerus* Bell *R. lacerus* Mutel = *pyrenaeus* L.)		14	Langlet	1936
R. lanuginosus? var. *flor. plen.*		14	Langlet	1927
R. millefoliatus Vahl.*		14	Langlet	1932
R. Nelsoni Gray		14	Larter	1932
R. platanifolius L.* (*R. aconitifolius* L.)		14	Langlet	1927
R. Villarsii DC.*		14	Langlet	1932
R. velutinus? (*R. velutinus* Schur = *lanuginosus* L. *R. velutinus* Tenore)		14	Langlet	1927
R. abortivus L.		16	Sorokin	1929
R. aconitifolius L.*		16	Langlet	1927
R. aconitifolius L.		16	Larter	1932
R. alpestris L.*		16	Langlet	1927
R. amplexicaulis L.*		16	Langlet	1927
R. asiaticus L.		16	Nakajima	1936
R. asiaticus superbus Hort.		16	Langlet	1927
R. Breyninus Crantz * (*R. nemorosus* DC.)		16	Langlet	1932
R. Broteri Freyn		16	Larter	1932
R. bulbosus L.*		16	Langlet	1927
R. bulbosus L.		16	Larter	1932
R. bulbosus L.* var. *femina*		16	Langlet	1927
R. bulbosus L.* var. *flor. plen.*		16	Langlet	1927
R. bullatus L.*		16	Langlet	1932
R. caucasicus? (*R. caucasicus* Boiss. & Buhse = *Buhsei* Boiss. *R. caucasicus* Bieb.)		16	Langlet	1927
R. chinensis Bunge * (*R. pensylvanicus* L.)		16	Langlet	1936
R. chius DC.		16	Gregory	unpubl.
R. cortusaefolius Willd.*		16	Langlet	1936
R. crenatus? (*R. crenatus* Bertol. = *bilobus* Bertol. *R. crenatus* Waldst. & Kit.)		16	Langlet	1936
R. cymbalaria Pursh *		16	Langlet	1927

Name	*n*	2*n*	Author	Date
R. cymbalaria Pursh		16	Larter	1932
R. ficaria L.*		16	Langlet	1936
R. ficaria L.* *bulbillifera*		16	Langlet	1936
R. ficaria L.* *flor. plen.*		16	Langlet	1927
R. glacialis L.*		16	Langlet	1932
R. Gouanii Willd.		16	Larter	1932
R. gramineus L.		16	Larter	1932
R. graminifolius Salisb.* (*R. gramineus* L.)		16	Langlet	1927
R. hakkodensis Nakai		16	Matsuura & Suto	1935
R. hederaceus L.	8		Boecher	1932
R. heucheraefolius Presl * (*R. palustris* L.)		16	Langlet	1936
R. lapponicus L.*		16	Langlet	1932
R. lapponicus L.		16	Flovik	1936
R. montanus? (*R. montanus* Orsini = *Villarsii* DC. *R. montanus* Presl = *acris* L. *R. montanus* Sibth. & Sm. = *Sibthorpii* Boiss. *R. montanus* Willd.)		16	Langlet	1932
R. Nelsoni Gray	8		Gregory	unpubl.
R. nemorosus DC.*		16	Langlet	1932
R. nemorosus DC. *polyanthemoides*		16	Gregory	unpubl.
R. nyssanus Leichtl.*		16	Langlet	1927
R. ophioglossifolius Vill.*		16	Langlet	1927
R. ophioglossifolius Vill.		16	Larter	1932
R. orientalis L.*		16	Langlet	1932
R. oxyspermus Ross.		16	Larter	1932
R. polyanthemus L.		16	Larter	1932
R. pygmaeus Wahlenb.*		16	Langlet	1932
R. pygmaeus Wahlenb.		16	Flovik	1936
R. quelpaertensis Nakai		16	Matsuura & Suto	1935
R. rhomboideus Goldie (*R. ovalis* Raf.)	8	16	Coonen	1939
R. sardous Crantz *	8		Langlet	1932
R. sardous Crantz	8		Larter	1932
R. scoticus E. S. Marshal *		16	Langlet	1932
R. Seguieri Vill.*		16	Langlet	1932
R. Sprunerianus Boiss.		16	Larter	1932

Name	*n*	2*n*	Author	Date
R. Thora?		16	Langlet	1932
(*R. Thora* Sibth. & Sm.				
= *brevifolius* Tenore				
R. Thora Sturm				
= *hybridus* Biria				
R. Thora Weizel.				
auricomus L.				
R. Thora L.)				
R. Vernyi Franch. & Sav.		16	Matsuura & Suto	1935
R. calandrinioides Oliver *		ca. 18	Coonen	1939
R. acer L.* var. *tetrpl.*		28	Langlet	1932
R. auritiifolius (author?)	14		Larter	1932
R. californicus Benth.*		28	Coonen	1939
R. Hornemanni Schlecht.*		28	Langlet	1936
R. kerneri Freyn	14		Larter	1932
R. kerneri Freyn		28	Matsuura & Suto	1935
R. lanuginosus?		28	Bruun	?
(*R. lanuginosus* Amo				
= *nemorosus* DC.				
R. lanuginosus Costa				
= *sardous* Crantz				
R. lanuginosus Ledeb.				
= *acris* L.				
R. lanuginosus Boiss. & B.				
= *constantinopalitanus* Urv.				
R. lanuginosus Pursh				
= *repens* L.				
R. lanuginosus Walt.				
= *recurvatus* Poir				
R. lanuginosus L.)				
R. macrophyllus?		28	Langlet	1936
(*R. macrophyllus* Desf.				
= *palustris* L.				
R. macrophyllus Ledeb.				
= *grandiflorus* L.				
R. macrophyllus Schur				
= *acris* L.)				
R. occidentalis?		28	Langlet	1936
(*R. occidentalis* Torr. & Gray				
= *Nelsoni* Gray				
R. occidentalis Freyn				
R. occidentalis Nutt.)				
R. parviflorus L.*		28	Langlet	1927

Name	*n*	2*n*	Author	Date
R. parviflorus L.		28	Jane	1932
R. parviflorus L.		28	Larter	1932
R. pedatus Waldst. & Kit.		28	Larter	1932
R. rupestris Guss.		28	Larter	1932
R. serbicus Vis.		28	Larter	1932
R. serbicus Vis.*		28	Langlet	1936
R. Sommieri Alboff *		28	Langlet	1936
R. tuberosus?		28	Langlet	1936
(*R. tuberosus* Hornem. = *Hornemanni* Schlecht. *R. tuberosus* Lapeyr. = *nemorosus* DC. *R. tuberosus* Schur = *montanus* Willd. *R. tuberosus* Stur = *acris* L.)				
R. aquaticus Neck.* (*R. aquatilis* L.)		32	Boecher	1932
R. arvensis L.*		32	Langlet	1927
R. arvensis L.		32	Larter	1932
R. asiaticus L.		32	Larter	1932
R. asiaticus L. var. *turban grandiflora*		32	Larter	1932
R. auricomus L.*		32	Langlet	1932
R. auricomus L.		32	Larter	1932
R. auricomus L.		32	Gregory	unpubl.
R. Baudotii Godr.*	16		Boecher	1932
R. cassubicus L.*		32	Langlet	1932
R. cassubicus L.		32	Lewitsky	1934
R. fascicularis Muhl.		32	Coonen	1939
R. ficaria L.*		32	Langlet	1927
R. ficaria L.		32	Larter	1932
R. ficaria L. var. *incumbens* Schultz		32	Larter	1932
R. ficaria L. *euficaria* Briq.		32	Hocquette	1922
R. ficaria L. var. *ochroleuca*		32	Langlet	1927
R. flabellatus Desf. (*R. chaerophyllus* L.)		32	Larter	1932
R. flammula L.*		32	Langlet	1927
R. flammula L.		32	Larter	1932
R. flammula L.		32	Matsuura & Suto	1935
R. flammula L.		32	Gregory	unpubl.
R. hyperboreus Rottb.*		32	Langlet	1936
R. hyperboreus Rottb.		32	Flovik	1936

Name	*n*	2*n*	Author	Date
R. illyricus L.*		32	Langlet	1927
R. illyricus L.		32	Larter	1932
R. Lenormandii Schultz		32	Larter	1932
R. lomatocarpus Fisch. & Mey.*		ca. 32	Langlet	1936
R. lomatocarpus Fisch. & Mey.		32	Gregory	unpubl.
R. monspeliacus?		32	Langlet	1932
(*R. monspeliacus* Georgi = *illyricus* L. *R. monspeliacus* L. *R. monspeliacus* Winkl. = *Winkleri* Freyn)				
R. monspessulanus Jord. (*R. monspeliacus* L.)		32	Coonen	1939
R. Pallasii Schlecht.		32	Flovik	1936
R. parnassifolius L.*		32	Langlet	1936
R. peltatus Schrank		32	Larter	1932
R. psilostachys Griseb.		32	Larter	1932
R. pyrenaeus?		32	Langlet	1932
(*R. pyrenaeus* Gouan = *Gouani* Willd. *R. pyrenaeus* L.)				
R. recurvatus Poir.		32	Coonen	1939
R. repens L.*		32	Langlet	1927
R. repens L.	16		Larter	1932
R. repens L.	16		Bruun	?
R. repens L.		32	Matsuura & Suto	1935
R. repens L.* *flor. plen.*		32	Langlet	1927
R. repens L. var. *typicus* Beck.		32	Hocquette	1922
R. reptans L.*		32	Langlet	1927
R. reptans L.* (*R. flammula* L.)		32	Boecher	1938
R. sceleratus L.*		32	Langlet	1936
R. sceleratus L.		32	Coonen	1939
R. sceleratus L.		32	Gregory	unpubl.
R. septentrionalis?		32	Coonen	1939
(*R. septentrionalis* Poir. = *repens* L.? *R. septentrionalis* De Bray)				
R. sericeus?		32	Langlet	1936
(*R. sericeus* Poir. *R. sericeus* Willd. = *illyricus* L.)				
R. trachycarpus Fisch. & Mey.*		32	Langlet	1927
R. falcatus L.*		40	Langlet	1932

Name	*n*	2*n*	Author	Date
R. constantinopolitanus Urv.		42	Larter	1932
R. trilobus Desf.		42	Larter	1932
R. apiifolius?		48	Langlet	1932
(*R. apiifolius* Desf. = *monspeliacus* L. *R. apiifolius* Pers. *R. apiifolius* St. Lag. = *sceleratus* L.)				
R. auricomus L. var.		48	Bruun	?
R. muricatus L.*		48	Langlet	1927
R. muricatus L.		48	Larter	1932
R. muricatus L.		48	Gregory	unpubl.
R. nivalis L.		48	Flovik	1936
R. trilobus Desf.*		48	Langlet	1927
R. trilobus Desf.		48	Gregory	unpubl.
R. nivalis?		56	Langlet	1932
(*R. nivalis* Lag. = *demissus* DC. *R. nivalis* Lerchew. = *montanus* Willd. *R. nivalis* Pall. = *polyrhizos* Steph. *R. nivalis* Sibth. & Sm. = *Sibthorpii* Boiss. *R. nivalis* L.)				
R. septentrionalis Poir. (*R. repens* L.)		64	Gregory	unpubl.
R. sulphureus Soland.		ca. 80	Flovik	1936
R. sulphureus Soland.*		96	Langlet	1936
R. sulphureus Soland. (*R. nivalis* L.)		96	Flovik	1940
R. lingua L.		128	Langlet	1932

Ranunculus is the largest genus in the family and has been more thoroughly investigated cytologically than any other genus. A considerable amount of work has been done on the cytological and genetic behavior of monoecious, dioecious, and gynodimorphic races of *R. acris* especially by Sorokin (1927) and Whyte (1929). This species is extremely variable from the standpoint of chromosome numbers and is not characteristic of other species of the genus. More general works on the genus have been those of Langlet (1927) and (1936), Larter (1932), Flovik (1936), and Coonen (1939). Polyploidy is the rule in the genus both within the 8- and 7-chromosome series. It is in this genus that the frequency of aneuploid 7-chromosome types becomes numerous enough to challenge the assumption of an 8 basic number for the genus. When the rest of the family with Ranunculus-type chromosomes is considered and especially the similar situation in *Anemone* it becomes

evident that 7 is probably the derived number. (See graph comparing the 7- and 8-series in *Ranunculus*, text Fig. 2.)

Genus: *Batrachium* S. F. Gray (*Ranunculus*). Large Ranunculus-type chromosomes. *n*-numbers = 8, 16.

Name	*n*	2*n*	Author	Date
B. hederaceum S. F. Gray * (*R. hederaceus* L.)		16	Langlet	1927
B. paucistamineum Schultz * (*R. trichophyllus* Chaix)		16	Langlet	1927
B. marinum Fries * (*R. Baudotii* Godr.)		32	Langlet	1927

Genus: *Ficaria* Hall (*Ranunculus*). Large Ranunculus-type chromosomes. *n*-number = 8.

Name	*n*	2*n*	Author	Date
F. verna Huds.	8		Negodi	1930
F. verna Huds.	8	16	Larter	1932
F. verna Huds.* (*R. Ficaria* L.)		16	Boecher	1932

Genus: *Thalictrum* L. (76) N. Hem. Small Thalictrum-type chromosomes. *n*-numbers = 7, (12)?, 14, 21, (24)?, 28, 35, 42, 56, 77. Pl. XII, Figs. 124–131.

Name	*n*	2*n*	Author	Date
T. alpinum L.*		14	Langlet	1927
T. alpinum L.		14	Sakai	1935
T. aquilegifolium L.*		14	Langlet	1927
T. aquilegifolium L.	7		Matsuura & Suto	1935
T. aquilegifolium L.		14	Kuhn	1928
T. aquilegifolium L. *atropurpureum*		14	Kuhn	1928
T. foetidum? (*T. foetidum* Gouan = *minus* L. *T. foetidum* L.)		14	Langlet	1927
T. foetidum L.		14	Kuhn	1928
T. foliosum?		14	Langlet	1936
T. montanum Wall. (*T. minus* L.)	7	14	Kuhn	1928
T. petaloideum L.		14	Kuhn	1928
T. przewalski Maxim.		14	Kuhn	1928
T. Yezoense Nakai	7		Matsuura & Suto	1935
T. purpurascens L.	12	24	Kuhn	1928
T. angustifolium? (*T. angustifolium* Pollich = *simplex* L. *T. angustifolium* L.)		28	Langlet	1927

Name	*n*	2*n*	Author	Date
T. aquilegifolium L.		28	Kuhn	1928
T. aquilegifolium L. var. *hybridum* Hort.		28	Langlet	1927
T. bulgaricum Velen.		28	Kuhn	1928
T. corynellum DC.		28	Kuhn	1928
T. dipterocarpum Franch.*		28	Langlet	1927
T. dipterocarpum Franch.		28	Kuhn	1928
T. elatum Jacq. (*T. minus* L.)		28	Kuhn	1928
T. exaltatum? (*T. exaltatum* Gaud. = *flavum* L.? *T. exaltatum* C. A. Mey. = *simplex* L.)		28	Kuhn	1928
T. Fendleri? (*T. fendleri* C. L. Anders. = *polycarpum* S. Wats. *T. Fendleri* Engelm.)		28	Langlet	1927
T. Fendleri Engelm.	14	28	Kuhn	1928
T. flavum L.		28	Gregory	unpubl.
T. galioides Nestl.		28	Kuhn	1928
T. glaucum? (*T. glaucum* Sieber = *corynellum* DC. *T. glaucum* Desf.)		28	Langlet	1927
T. glaucum Desf.		28	Kuhn	1928
T. lucidum L.*		28	Langlet	1927
T. lucidum L.	14	28	Kuhn	1928
T. lucidum L.* var. *laserpitiifolium*		28	Langlet	1927
T. majus Crantz		28	Gregory	unpubl.
T. mediterraneum Jord.* (*T. angustifolium* L.)		28	Langlet	1927
T. medium Jacq.* (*T. minus* L.)		28	Langlet	1927
T. rufinerve Lej. & Court (*T. flavum* L.)		28	Kuhn	1928
T. rugosum Ait.		28	Kuhn	1928
T. tuberosum L.		28	Kuhn	1928
T. exaltatum?		35	Kuhn	1928
T. sp.		35	Langlet	1927
T. anemonoides Michx.	(35–37)	42	Kuhn	1928
T. banaticum Rochel?		42	Kuhn	1928
T. calabricum Spreng.*		42	Langlet	1927

Name	*n*	2*n*	Author	Date
T. calabricum Spreng.		42	Kuhn	1928
T. chelidonii DC.		42	Kuhn	1928
T. confine Fernald		42	Kuhn	1928
T. cornuti?		42	Langlet	1927
(*T. cornuti* Poir. = *minus*? *T. cornuti* Torr. & Gray = *corynellum* DC. *T. cornuti* L.)				
T. cultratum Wall.		42	Kuhn	1928
T. Delavayi Franch.*		42	Langlet	1927
T. Delavayi Franch.		42	Kuhn	1928
T. dioicum L.		42	Kuhn	1928
T. flexuosum Bernh.	21	42	Kuhn	1928
T. javanicum Blume		42	Kuhn	1928
T. maximum?		42	Kuhn	1928
T. minus L.*		42	Langlet	1927
T. minus L.	21	42	Gregory	unpubl.
T. minus L.* *Kochii*		42	Langlet	1927
T. minus L.* *odoratum*		42	Langlet	1927
T. orientale Boiss.		42	Kuhn	1928
T. pauciflorum?		42	Langlet	1927
(*T. pauciflorum* Rafin. = ? *T. pauciflorum* Schur = *aquilegifolium* L. *T. pauciflorum* Steph. = *simplex* L. *T. pauciflorum* Royle)				
T. purpurascens?		42	Langlet	1927
(*T. purpurascens* DC. = *dioicum* L. *T. purpurascens* Georgi = *minus* L.)				
T. rubellum Sieb. & Zucc.* (*T. aquilegifolium* L.)		42	Langlet	1927
T. sparsiflorum Turez.		42	Kuhn	1928
T. squarrosum Steph.		42	Kuhn	1928
T. minus L. subsp. *dunense*		48	Hocquette	1922
T. rariflorum Fries *		56	Langlet	1927
T. simplex?		56	Langlet	1927
(*T. simplex* DC. = *flavum* L. *T. simplex* L.)				

Name	n	$2n$	Author	Date
T. coriaceum Small		70	Gregory	unpubl.
T. kemense Fries * (*T. minus* L.)		70	Langlet	1927
T. przewalski Maxim.*		70	Langlet	1927
T. simplex L.	35	70	Kuhn	1928
T. flavum L.*		84	Langlet	1927
T. flavum L.		84	Kuhn	1928
T. rariflorum Fries *		112	Langlet	1927
T. simplex?		112	Langlet	1927
T. revolutum DC.		ca. 133	Gregory	unpubl.
T. polygamum Muhl.	(74)	154	Gregory	unpubl.
T. polygamum Muhl.		154?	Kuhn	1933

Polyploidy reaches the maximum development in the family in *Thalictrum*, there being an almost continuous range of numbers represented from $n = 7$ to $n = 77$. The highest polyploid species in the family is also found in this genus with *Thalictrum polygamum* $2n = 154$. The genus is also remarkable in that of the small Thalictrum-type chromosome genera this is the only one that shows any marked degree of polyploidy. It can be seen that so far as polyploidy affects speciation this genus represents a developmental peak in the small chromosome group and that *Ranunculus* holds the same position in the large chromosome group. The systematic position of *Thalictrum*, viz. grouped with *Anemone*, *Clematis*, and *Ranunculus*, is quite untenable from a cytological point of view.

Genus: *Adonis* L. (20) Eur. As. Large Ranunculus-type chromosomes. n-numbers = 8, 12, 16, 20. Pl. I, Figs. 7, 8.

Name	n	$2n$	Author	Date
A. apennina? (*A. apennina* L. = *vernalis* L. *A. apennina* Pall. = *wolgensis* Stev. *A. apennina* Schouw = *pyrenaica* DC.)		16	Langlet	1927
A. pyrenaica? (*A. pyrenaica* Hook. f. & Thoms. = *chrysocyathus* Hook. f. & Thoms. *A. pyrenaica* DC.)	8		Langlet	1927
A. vernalis? (*A. vernalis* Asso = *dentata* Delile *A. vernalis* L.)	8		Langlet	1927
A. wolgensis? × vernalis?		16	Langlet	1927
A. hahurica (author?)	12		Ishikawa	1916

Name	*n*	2*n*	Author	Date
A. hahurica (author?)	12		Takamine	1916
A. hahurica (author?)		24	Langlet	1927
A. aestivalis?		32	Langlet	1927
A. aestivalis?		32	Gregory	unpubl.
(*A. aestivalis* Bieb. = *autumnalis* L. *A. aestivalis* Link, = *microcarpa* DC. *A. aestivalis* L.)				
A. autumnalis?		32	Langlet	1927
A. autumnalis?		32	Gregory	unpubl.
(*A. autumnalis* Bieb. = *aestivalis* L. *A. autumnalis* L.)				
A. flammea?	16		Langlet	1927
(*A. flammea* Schleich. = *aestivalis* L. *A. flammea* Jacq.)				
A. vernalis? var. *amurensis*	20		Sugiura	1931
A. vernalis? var. *amurensis*	20		Sugiura	1936

Discussion

Polyploidy in the Ranunculaceae

Polyploidy as an active force in the evolution and creation of new species in the higher plants has received a great deal of attention during the last decade. There has been some controversy over the relative effects of auto- and allopolyploidy. Müntzing (1936) published a comprehensive review of the literature and the results of his own work on the evolutionary significance of autopolyploidy. No comprehensive review of this extensive subject will be attempted here, but a few of the more significant concepts will be brought forward in an effort to evaluate the significance of polyploidy in the Ranunculaceae. Müntzing suggests that at least 50% or more of angiosperm species are polyploid. He reviews various authors' opinions of the effects of polyploidy on speciation. These extend from the extreme view that new polyploid species cannot possibly arise from the multiplication of the same genom through the more mild opinions that secondary rearrangements in autopolyploids account for new species, to those which have considered autopolyploidy as one of the major forces in the production of new species. Müntzing himself makes a special point of the production of allopolyploids from autopolyploids by means of chromosomal changes and through hybridization. Autopolyploidy as a means of a new starting point in the evolution of a race through limitation of crossing between the polyploids and their diploid ancestors is emphasized. He especially emphasizes (in regard to the preponderance of polyploidy in perennial species over annual species) that "the evolution of these species has essentially been caused by quantitative chromosome alterations," that whether this quantitative increase is allo- or autopolyploidy is a matter of minor importance,

"We have reason to believe that the effect observed is chiefly due to the reduplication of entire genoms." Müntzing's concluding remark is, "thus it is evident that quantitative chromosome alterations have played a very important rôle in the evolution of the higher plants." Although this author weighs very carefully the opinions of others and the evidence from natural and induced polyploidy and several times succeeds in making the distinction between allo- and autopolyploidy extremely nebulous, there is no doubt he considers the formation of autopolyploid chromosome races an important factor in the evolution of new species.

Stebbins (1940), however, challenges the rôle of autopolyploidy in plant evolution. He points out that the mutation rate as measured by visible mutations is much slowed down in polyploids, less frequent in tetraploids than in diploids, still less in hexaploids, and practically negligible in octaploids. He challenges the idea that an isolated autopolyploid is potentially a progenitor of a new race. The intersterility of polyploids with their diploid progenitors and especially of such triploid hybrids as do occur between them together with the stabilizing effects of apomixis in polyploids tends to isolate and fix autopolyploid races, thus leading to what might be termed an evolutionary dead end. But, here comes into play the much discussed influence of amphidiploidy. Do such chromosomally doubled hybrids, allopolyploids, give rise to new evolutionally significant races? Regardless of the obvious importance of such new fertile "species" to horticulture and agriculture and regardless of the obvious and immediate channels for theory that they open up little is definitely known as to their importance in plant evolution.

Müntzing (1936) and others have proposed to distinguish between allo- and autopolyploids by one means or another, especially by the behavior of the chromosomes at meiosis, but the fact remains that so far as actual knowledge of allo- and autopolyploidy is concerned, their relative frequencies in the plant kingdom at large are still mainly a matter of conjecture.

Stebbins has however brought into focus in the special connection of polyploidy the keen distinction that must be made between evolution of forms on the one hand and their speciation on the other. Since the two are so intimately related historically, the fact of speciation and the presence of multiform groups of organisms having been the factual basis out of which the theory of evolution grew, it is difficult to make this distinction clear. If evolution is to be taken simply as a matter of change then it becomes impossible to distinguish them. However, if evolution is to mean anything in respect to perpetuation by change and consequent adaptation of living organisms on the earth, then it must be distinguished from its necessary by-product speciation. Speciation involves the idea of the production of more or less stable clearly distinguishable types whereas evolution presupposes plasticity or capability of change. Thus we are confronted with the confusion that comes from the different kinds of change mechanisms that lead sometimes both to speciation and evolution and sometimes only to speciation. It appears to the writer significant that polyploidy as one of the means of change in type has been emphasized only in the plant world even though biologists consider the fundamental causes of evolution to be at work in plants and animals alike.

In the Ranunculaceae we have fortunately a plant family that goes to the extremes of stability and instability of chromosome number in two sections of the family widely separated cytologically. However, before the relative effects of polyploidy on speciation

and evolution within the two groups can be discussed an examination of the chromosome numbers must be made and a conclusion arrived at as to what shall constitute diploidy and polyploidy.

The following *n*-numbers occur in the Ranunculaceae: 5, 6, 7, 8, 9, 10, 12, 13, 14, 16, 18, 21, 24, 28, 32, 35, 42, 48, 56, 64, 77. Examination of this series of numbers alone would lead to great confusion in selecting a basic *x*-number for the family. If, however, the number of species in the family associated with each number is examined and a consideration is taken of the taxonomic groups within the family it is possible to select the important low numbers. Using the data in Table I as a basis the species become grouped in the following manner: 5*n*—21 species, 6*n*—9 species, 7*n*—56 species, 8*n*—185 species, 9*n*—2 species, 10*n*—12 species, 12*n*—4 species, 13*n*—1 species, 14*n*—33 species, 16*n*—79 species, 18*n*—1 species, 21*n*—21 species, 24*n*—10 species, 28*n*—3 species, 32*n*—4 species, 35*n*—4 species, 42*n*—1 species, 48*n*—2 species, 56*n*—2 species, 64*n*—1 species, 77*n*—1 species. If these numbers of species are collected under the low numbers and their higher multiples, within natural groups, they arrange themselves as follows: 5 and its multiples, 33 species; 6 and no multiples, 9 species; 7 and its multiples, 121 species; 8 and its multiples, 281 species; 9 and its multiples, 3 species; 13 and no multiples, 1 species. An occasional aberrant *n*-number such as 12 within the 7–8-*n* genus *Anemone* has not been included.

The numbers 5, 6, 7, 8, 9, and 13 stand out immediately as the *n*-numbers which have to be considered. One might suppose that here we have an aneuploid series of numbers which have secondarily given rise to large numbers of species based on these numbers. However, for taxonomic reasons the number 6 has been considered derived from 8 and not from a basic number 5 or 7. Also from taxonomic evidence it becomes apparent that we have here in the family Ranunculaceae an *x*-5 series, an *x*-7 series, an *x*-8 series with 7*n* derived and unrelated to the *x*-7 series, an *x*-9 and an *x*-13 series. The only genus where 7 might be considered the basic number in the large chromosome group is in the genus *Ranunculus* itself. However, on the evidence from the number of species in the 8 and 7 series in this genus it appears that 7 must be the derived and not the basic number (see text Fig. 2). For taxonomic reasons 13 is known not to be derived from an *x*-7 series by the loss of one chromosome by a 14 chromosome plant. Thus we are confronted with the taxonomically distinct groups of numbers: 5, 7, 8, 9, and 13. The only numbers left which can be considered as multiples of a prime number are 8 and 9. If the number 8 is considered to be derived from a basic *x*-4 as Langlet (1932) has done then the question of polyploidy in the family takes on added significance, for this group of species constitutes more than 40% of all the counted species of the family. According to Darlington (1937) in his discussion of polyploidy *x*-4 is probably correct. The number 4 has however nowhere been found in the Ranunculaceae and there is no more reason to believe that 8 is a derived polyploid simply because it chances to be divisible by 2 than there is to assume that 5, 7, and 13 are derived polyploids for which no such divisor can be found. It is obvious that some one or several low numbers must be considered as diploid and it appears to the writer more accurate to select such numbers as have been reported than some hypothetical figure simply for theoretical or arithmetical convenience (see Wanscher 1934). Consequently the following basic *x*-numbers have been assumed by the writer for the Ranunculaceae on the foundations of the classification discussed below: 5, 7, 8, 9, and 13, all representing distinct taxonomic units.

We are now ready to consider the genera from the x-7 and x-8 series which represent the extremes of stability and instability in chromosome numbers. These genera are *Clematis* and *Ranunculus* in the group with large Ranunculus-type chromosomes and *Aquilegia* and *Thalictrum* in the group with small Thalictrum-type chromosomes.

Clematis marks a peak of evolutionary development on the one hand and a high degree of speciation on the other. The development of the woody habit in the Ranunculaceae reaches its greatest perfection in this genus; it is almost if not the most widely geographically distributed genus in the family, growing not only in temperate and cold temperate regions of both hemispheres but in the tropics as well. It occurs in every big land mass of the earth except Antarctica not excepting Madagascar, Australia, New Zealand, the Malay peninsula, the Philippines, West Indies, the Fiji Islands, etc. It occurs from the highlands of Tibet and the tropics of India to northern Asia, over the length and breadth of the western hemisphere, Europe, the Mediterranean world and tropical and south Africa. In short, it has spread over the face of the earth and is represented by both deciduous and evergreen species and varies in life habit from practically perennial herbs and low shrubby bushes to tall climbing coarse woody vines. It is very close to the second largest genus in the family with 170 species with variety enough to be divided by some into two genera.

Although only about 40 of its 170 species have been studied every one but two were simple diploids with $n = 8$. Obviously polyploidy both as a factor in evolution and speciation is non-existent in this remarkable genus of plants.

Consider, on the other hand, the genus *Ranunculus*. From an evolutionary standpoint it is not more remarkable than one of several other genera in the family with a similar though not as complex situation as regards chromosome number. Its geographic distribution though wide is practically limited to the cool temperate northern hemisphere. Nevertheless, speciation has attained great development in the genus, it being the largest genus in the family with 250 species. No question can be raised but that its tremendous chromosome variability with n-numbers of 7, 8, 14, 16, 21, 24, 28, 32, 40, 48, and 64, has played a large part in the production of many forms. It has run the gamut of chromosome number variation with aneuploidy and polyploidy. What conclusions, however, can one draw concerning the importance of polyploidy in evolution and speciation in these two genera of the Ranunculaceae? Obviously *Clematis* is equally highly evolved and very nearly as highly diversified as to species as *Ranunculus*. In short can one from the limited experimental evidence at hand conclude because of the presence of polyploidy in a plant family that it has been one of the prime factors in the evolution or speciation of that family? If one be allowed to conjecture is it not conceivable that the tiny pappus-like bristles on the styles of *Clematis* fruits have been a much more significant factor in the wide distribution, even to small oceanic islands, and consequent subjection of the genic material to greater environmental influence and selection, than all the numerical variation of *Ranunculus* chromosomes combined?

Among the small Thalictrum-type chromosome genera the situation is very much the same in its general aspects but differs in some details. Here again speciation has been favored somewhat in the polyploid genus, there being about 76 species of *Thalictrum* and only about 50 in *Aquilegia* (some estimates include 80–100 species). In regard to evolution it is difficult to contrast the two as sharply as in the cases of *Clematis* and *Ranunculus* but

several points may be mentioned. In geographic distribution *Aquilegia* covers a tremendous territory in the northern hemisphere, growing from south-eastern China across northern and middle Asia through Europe to Spain. In North America it grows from Canada to Florida in the east and from the Canadian Rockies in the west to Mexico. Flower development reaches a peak in this genus, varying from the non-spurred species of China to the medium-spurred species of Europe to the longer spurred species of North

TABLE I

THE GROUPING OF *n*-CHROMOSOME-NUMBERS BY GENERA IN THE RANUNCULACEAE

The *n*-numbers occur by genera in the order that they appear in the Chromosome List, i.e., the first genus in the list in which $n = 8$ has 12 species with this number. Horticultural varieties, hybrids, and species of uncertain number have been omitted.

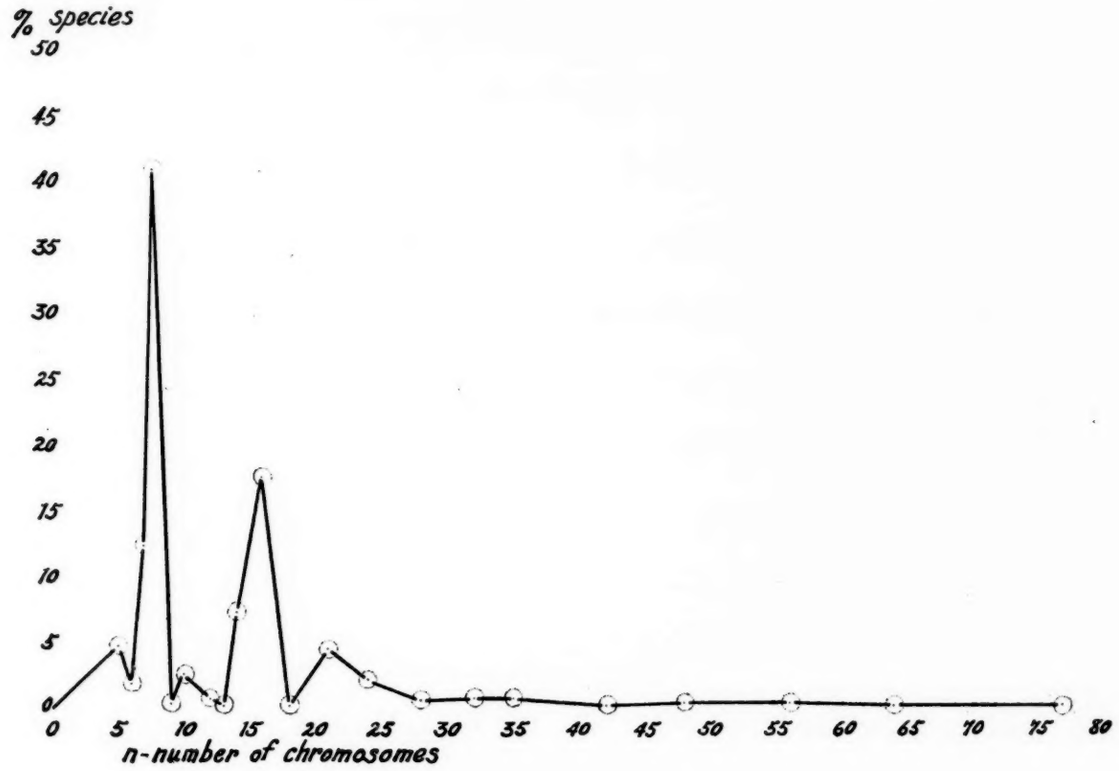
n-Chromosome No.	Number of Species by Genera	Total No. Species	% Species
5	21	21	4.7
6	9	9	2.0
7	1, 2, 19, 6, 1, 19, 8	56	12.4
8	12, 1, 2, 4, 8, 1, 19, 19, 35, 34, 1, 2, 41, 2, 1, 3	185	40.9
9	2	2	0.4
10	1, 11	12	2.7
12	3, 1	4	0.9
13	1	1	0.2
14	1, 1, 13, 18	33	7.3
16	1, 1, 2, 8, 12, 9, 15, 1, 26, 1, 3	79	17.5
18	1	1	0.2
21	2, 19	21	4.7
24	2, 1, 1, 1, 5	10	2.2
28	1, 2	3	0.7
32	2, 1, 1	4	0.9
35	4	4	0.9
42	1	1	0.2
48	1, 1	2	0.4
56	2	2	0.4
64	1	1	0.2
77	1	1	0.2
	Grand Total	452	100.0%

America. Floral evolution reaches its peak in the species of south-western N. America, especially in *A. longissima*. If hybridization can be considered as one of the primary factors in evolution *Aquilegia* is in a position to take advantage of all its possibilities. Species interfertility is the rule even between the most widely separated representatives of the genus and the F_1 hybrids of these crosses are remarkably fertile. It is noteworthy that sterility barriers appear immediately when one of its rare polyploid hybrids is crossed back to its diploid progenitors (Skalinska 1928).

The highest polyploid species in the family occurs in *Thalictrum* with *Thalictrum polygamum*, $2n = 154$. Polyploidy is the rule in this genus with the following *n*-numbers:

7, (12), 14, 21, (24), 28, 35, 42, 56, and 77. Furthermore of all the genera in the Ranunculaceae *Thalictrum* stands alone in the fact that more of its species are polyploid than diploid. (See graph comparing *Ranunculus* and *Thalictrum*, text Fig. 2.) Even though one cannot say that *Aquilegia* is better adapted or even that it has greater possibilities of evolution through hybridization, it can be said that *Aquilegia* has developed equally as successfully as *Thalictrum* without the aid of polyploidy.

In other words these four genera divided by two into the two great groups of the Ranunculaceae have exceptional development of polymorphism and geographic and

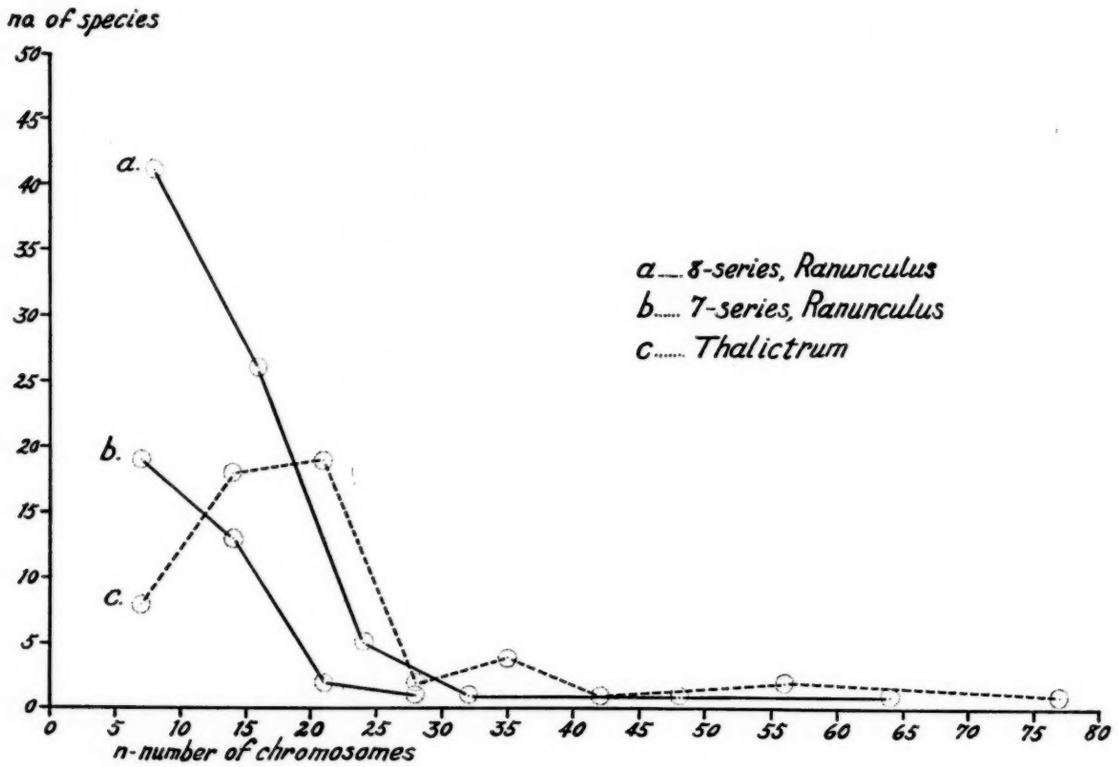


TEXT FIG. 1. Showing the *n*-numbers of chromosomes in the Ranunculaceae plotted against percentage of species having these numbers.

ecological distribution. In one of each group polyploidy has reached a maximum in the family and compares favorably with great polyploid genera of other families, in the other two, polyploidy is practically non-existent. Among the remainder of the family there are some small and apparently old and relatively unsuccessful genera. Some of these are stably polyploid and some stably diploid. In Table I and the graph in text Fig. 1, the relative frequency of diploids can be seen to be much greater than that of the polyploids. From these data one is forced to the conclusion that polyploidy in the Ranunculaceae, although it may have been a factor in the speciation of certain genera, cannot rank as one of the prime factors in the evolution of the family.

Cytology and Systematics

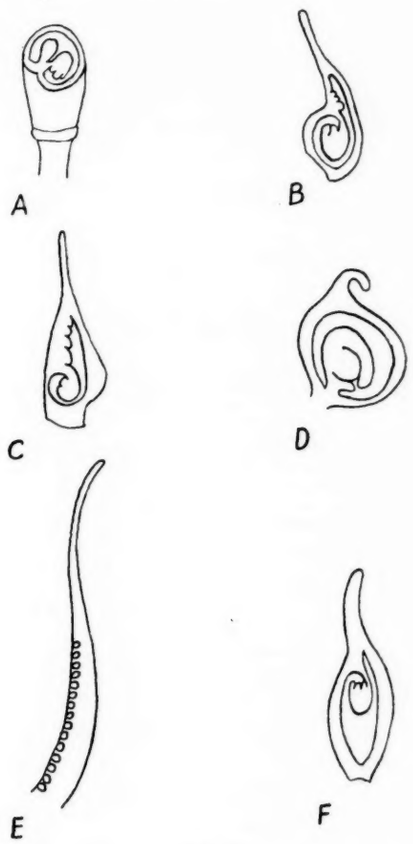
The family Ranunculaceae is a natural order of plants. This fact was emphasized by Jussieu (1773), who pointed out that although there could be no question as to the validity of the family as a group, classification within the family and its phylogenetic relationships were in great confusion because of the inability of his predecessors to select some one or few fundamental characteristics on which a natural classification could be based. This particular section of his paper could have been equally well written yesterday



TEXT FIG. 2. Showing *n*-numbers of chromosomes in the highest polyploid genera in the family, *Ranunculus* and *Thalictrum*, plotted against the number of species. Broken line shows *Thalictrum*, the two solid lines show the 7- and 8-series in *Ranunculus*.

except for Langlet's contribution (1932). Langlet noticed that the chromosomes of the Ranunculaceae fell very sharply into two great classes and suggested a reclassification of the family; he used this evidence to separate the family into two main subfamilies. However one may agree or disagree with the rank of his categories one must admit a major contribution to the classification of the family and perhaps a settlement of the difficulties which beset Jussieu. It is the purpose of this section to consider cytology as a tool of the taxonomist, to discuss the phylogenetic relationships in the Ranunculaceae, and to emphasize the importance of Langlet's work which has been either too much overlooked or misunderstood.

Cytology cannot be considered as a cure-all for all the taxonomic difficulties that beset the systematist. Anderson (1937) has ably pointed out the fact that in some plant groups it is of the first importance whereas in others, scarcely anything can be gained for the purposes of classification from an examination of the chromosomes. One of the earlier contributors to this subject fortunately had as material the polymorphic tribe of the Ranunculaceae, Prantl's Helleboreae (Lewitsky 1931). It was here that Lewitsky de-



TEXT FIG. 3. Diagrams of fruits from the two chromosome-type groups of the Ranunculaceae. *A. Delphinium*, *B. Anemone nemorosa*, *C. Clematis recta*, *D. Ranunculus*, in the Ranunculus-type chromosome group; *E. Aquilegia alpina*, *F. Thalictrum*, in the Thalictrum-type chromosome group. (*A*, *D*, and *F*, after Prantl (1891); and *B*, *C*, and *E*, after Rassner (1931).)

veloped the idea of the karyotype and using this mis-classified tribe arrived at some sound cytological conclusions. "The idea of the karyotype," to quote from Lewitsky, "as a karyological characteristic especially and exclusively applied to generic definitions or to any other definite systematic unit does not stand any critique. One cannot state what an extent of similarity of idiograms involves their subordination to the same karyotype. On the ground of larger or lesser community of characters, one may distinguish in one and the same complex of forms karyotypes of families, genera, species and races. Therefore the karyotype is a karyological characteristic of a group of allied forms, which may be

applied to any systematical unit." Thus it depends on the case at hand whether cytological characteristic differences observed apply to differences between races, species, genera, tribes, subfamilies, etc. In this respect cytological characteristics differ from external morphological structures as denoting certain rank in a systematic scheme.

However, it is too much to expect that these external characteristics should be equally applicable in the systematization of certain families such as the Ranunculaceae. It is here that an investigation into the cytology of the confused forms sometimes shows that there has been a parallel evolution of the external characters and that two sometimes more divergent groups of organisms may become grouped under one systematic unit. One of the most remarkable instances of this kind is to be found in the classification of *Yucca* and *Agave*. *Yucca* has a six-parted perianth, six stamens and a superior ovary which definitely places it in the family Liliaceae whereas *Agave* has a six-parted perianth, six stamens and an inferior ovary, which places it in the Amaryllidaceae. Even so, there is something almost persistently reminiscent of *Agave* when one is confronted with *Yucca*. Nevertheless, this floral characteristic, which is recognized to be of good taxonomic value in the rest of the genera in the two families, separates them. Examination however of the chromosomes of *Yucca* and *Agave* convincingly allies *Yucca* with *Agave* and not with the Liliaceae (McKelvey and Sax 1933).

In the Ranunculaceae we are confronted with a very similar situation. The taxonomic characters of follicular versus achene fruits group together genera which not only look very differently vegetatively but behave differently under cultural conditions. This would lead one to suspect some fundamental distinction to exist, but efforts of systematists to discover this distinction failed to reveal it in external morphology. However, no sooner had Langlet made his observations on the chromosomes than this situation resolved itself into a matter of parallel fruit development in two very different groups of the Ranunculaceae.

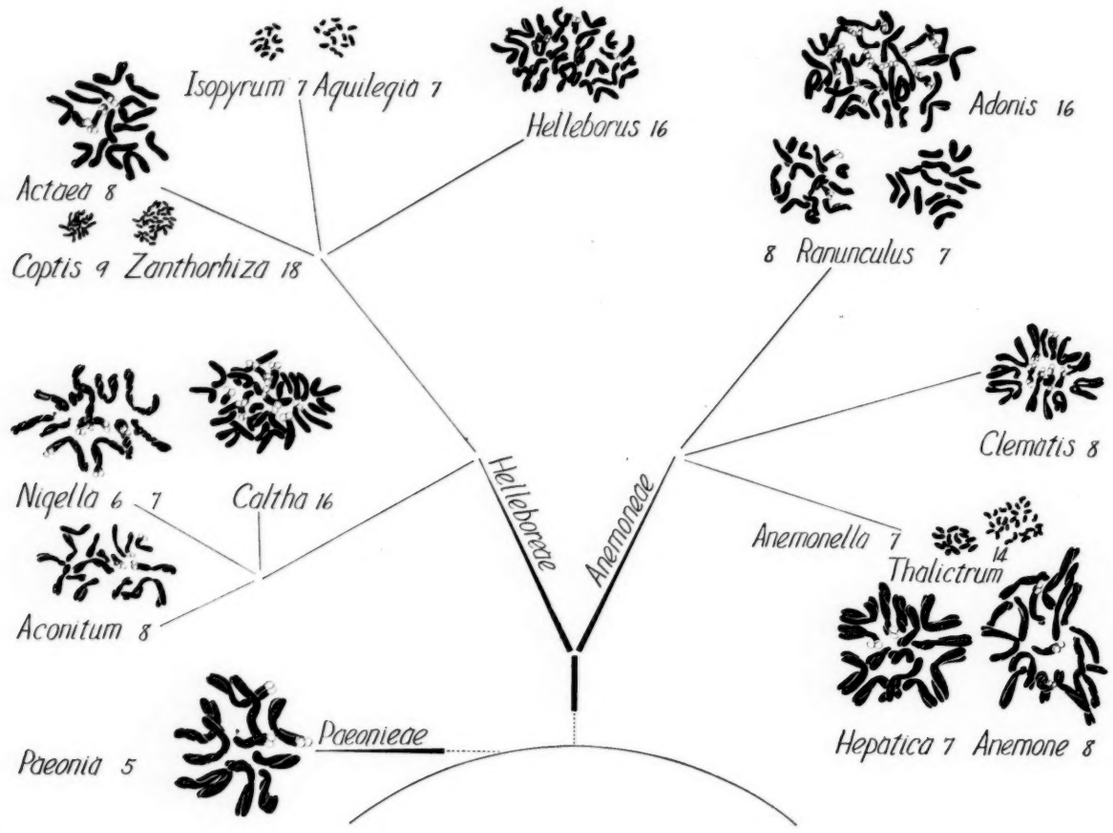
The genera of the Ranunculaceae divide themselves up as follows according to the two types of chromosomes and according to x-number. They are shown below along with the tribes with which they are usually associated.

Large Ranunculus-type chromosomes $x = 8$ ($7n$ derived in Anemone and Ranunculus and $n = 6$ and 7 in Nigella)	Caltha	Helleboreae
	Trollius	Helleboreae
	Callianthemum	Helleboreae
	Helleborus	Helleboreae
	Eranthis	Helleboreae
	Nigella	Helleboreae
	Actaea	Helleboreae
	Delphinium	Helleboreae
	Aconitum	Helleboreae
	Anemone	Anemoneae
	Clematis	Anemoneae
	Ranunculus	Anemoneae
	Adonis	Anemoneae
Small Thalictrum-type chromosomes $x = 7$	Isopyrum	Helleboreae
	Aquilegia	Helleboreae
	Thalictrum	Anemoneae
	Anemonella	Anemoneae

Small (type?) chromosomes $x = 9$	Coptis	Helleboreae
	Zanthorrhiza	Helleboreae
Large (type?) chromosomes $x = 5$	Paeonia	Paeonieae
$x = 10, 13$	Glaucidium	Hydrastideae
	Hydrastis	Hydrastideae

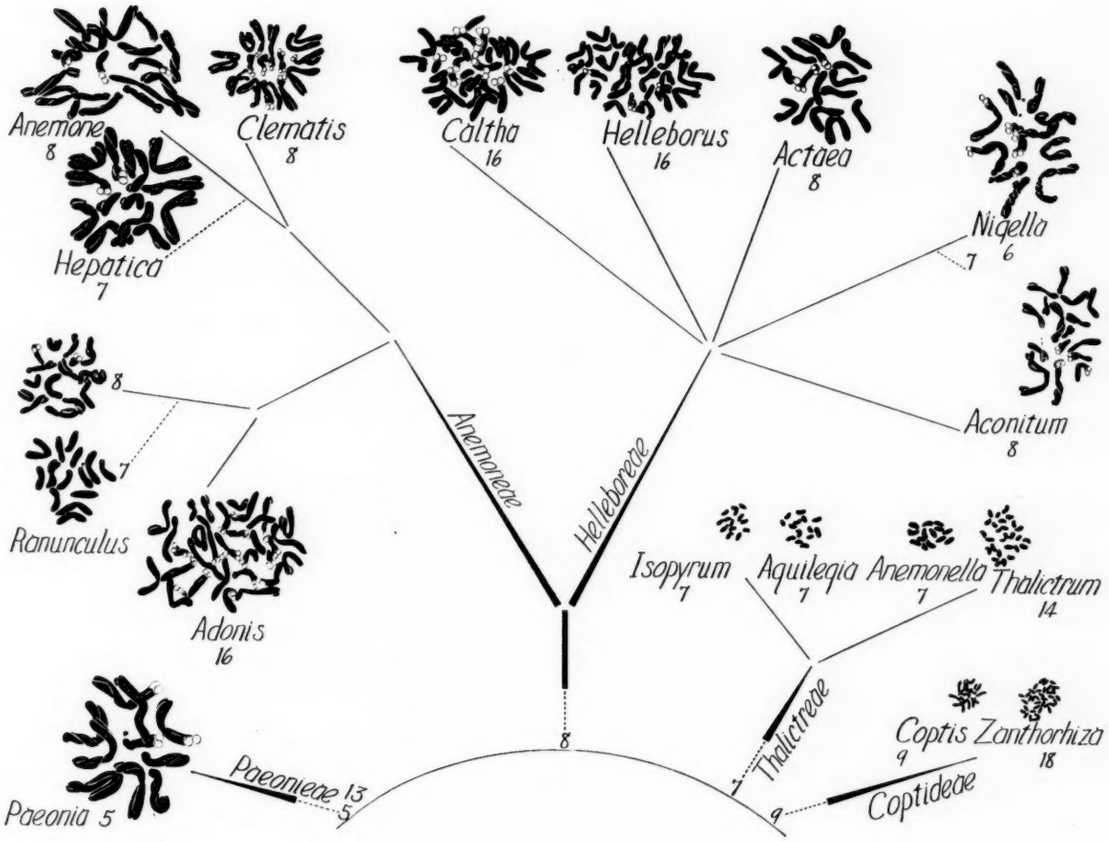
The above grouping, as can be seen from the tribal names occurring beside the genera, confuses the achene fruited and follicular fruited Ranunculaceae to a great extent. In order to show that this grouping also indicates natural relationships a comparison of the two classifications and their bases requires examination. The positions of the Paeonieae and the Hydrastideae in the above grouping are the same as those in the classical grouping of Engler and Gilg. The relation between the Helleboreae and the Anemoneae of these authors is somewhat disturbed. The basis for differentiating the Anemoneae and Helleboreae is the type of fruit. In text Figure 3 are fruit diagrams of some representatives of these two groups. Figures *A*, *B*, *C*, and *D* show the evolution from a follicular fruit to an achene fruit in the Ranunculus-type chromosome group. Figures *E* and *F* show the same conditions arrived at in the Thalictrum-type chromosome group without the intermediate steps. From these diagrams it is readily seen that the real gap between the follicular and achene fruited types within the Ranunculus-type group is not very great; and that the genera within this group are in reality closely related as to type of fruit. It merely becomes a matter of deciding which character is more significant for the primary division of the Ranunculaceae into tribes. In the light of the interrelation of the types of fruit and the great divergence of the chromosome-types it is the opinion of the writer that chromosome-type, in the Ranunculaceae, is a character of broader taxonomic scope than the fruit characters mentioned above and should therefore be used as a basis for the primary divisions of the family. This does not mean that the fruit characters be thrown out as a taxonomic factor but only that they be lowered in rank to secondary position to classify further the genera assigned to the groups delimited by the chromosome-type character. This is essentially what Langlet suggested in 1932 and the following quotation from Kumazawa (1938), who has worked on the morphology etc., of the Ranunculaceae for the last ten years, characterizes the reluctance with which some morphologists relinquish a floral or fruit character as fundamental for classification. "Especially the system of Langlet's is most open to criticism, for he, considering the karyotype of each genus, put the multiovular genera such as *Isopyrum*, *Aquilegia* and *Coptis* together with the uniovular genus *Thalictrum* into the Thalictroideae, and the multiovular genera such as *Helleborus*, *Trollius*, *Delphinium*, *Nigella*, *Aconitum*, *Cimicifuga* also together with the uniovular genera such as *Ranunculus*, *Clematis*, *Anemone* into the Ranunculoideae." The value of this criticism can be estimated by reference to Phylogenetic Charts I and II and to the fruit diagrams in Figure 3.

In the present arrangement of genera in the Ranunculaceae some significant changes have been made in the system of Langlet (1932), based chiefly on Langlet's own remarks on the chromosomes of *Coptis* and *Zanthorrhiza*. Langlet included the Coptideae in the small Thalictrum-type chromosome group even though he realized the significant morphological differences between *Coptis* and *Zanthorrhiza* on the one hand and *Thalictrum*,



PHYLOGENETIC CHART I. Showing the author's arrangement of the genera by tribes according to the Engler system.

Anemonella, *Isopyrum*, and *Aquilegia* on the other by placing them in separate tribes under his subfamily Thalictroideae. Furthermore, in his description of the chromosomes of *Coptis* and *Zanthorrhiza* Langlet remarks that although they resemble those of *Thalictrum*, etc. in size they are distinctly long and slender rather than bean-shaped as in the case of the latter. This chromosomal distinction between the two groups is borne out by gross morphological differences in life habit, vegetative characters, and by differences in fruit. *Coptis* is also distinguishable from *Zanthorrhiza* by the number of ovules. *Paeonia* is here included in the family Ranunculaceae as well as *Glaucidium* and *Hydrastis*. The position of *Paeonia* in the phylogenetic scheme of the writer is stated but since neither the genus *Hydrastis* nor *Glaucidium* has been examined by the writer their position in the scheme is left uncertain. Furthermore the present system allows a more reasonable correlation between gross morphology, chromosome-type and basic chromosome number within the family. Instead of grouping all the genera under two subfamilies and omitting the Paeonieae entirely and then making tribal distinctions within the subfamilies the tribes represented by distinct chromosome-type or basic number or both are considered to have equal taxonomic rank and to have arisen from an ancestral Ranunculaceae in which the



PHYLOGENETIC CHART II. Showing the author's own arrangement of the genera by tribes based on chromosome-type, basic number, and the type of fruit.

morphology and cytology are unknown. How the different chromosome-types and basic numbers arose in this ancestral group is not surmised.

The following classification represents what the writer considers the most natural grouping of the Ranunculaceae, exclusive of the Hydrastideae, that is possible at present. It is represented in graphic form in Phylogenetic Chart II and contrasted with the Engler system represented in Phylogenetic Chart I.

A. Large Ranunculus-type? chromosomes. Basic number = 5

Tribe I. Paeonieae

1. Paeonia

B. Large Ranunculus-type chromosomes. Basic number = 8

a. Fruit follicle, capsule, or berry

Tribe II. Helleboreae

2. Caltha
3. Trollius
4. Helleborus
5. Eranthis

6. Nigella
7. Actaea
8. Cimicifuga
9. Anemonopsis
10. Delphinium
11. Aconitum

b. Fruit an achene, usually one-seeded

Tribe III. Anemoneae

12. Anemone
13. Clematis
14. Ranunculus
15. Callianthemum
16. Adonis

C. Small Thalictrum-type chromosomes. Basic number = 7

Tribe IV. Thalictreae

i. Fruit follicular, many seeded

17. Aquilegia
18. Isopyrum

ii. Fruit an achene, one seeded

19. Anemonella
20. Thalictrum

D. Small slender (Coptis-type) chromosomes. Basic number = 9

Tribe V. Coptideae

i. Fruit several seeded

21. Coptis

ii. Fruit two seeded

22. Zanthorrhiza

E. (Not examined by writer)

Tribe VI. Hydrastideae (position uncertain)

Summary

1. The phylogeny and systematics of the Ranunculaceae have been studied from a cytological viewpoint, chiefly on the basis of the type and number of chromosomes.

2. A list of chromosome numbers with the genera listed within tribes according to the Engler system has been prepared from the literature and from the author's own work. The new chromosome numbers of 43 species involving 8 genera have been reported for the first time: *Aconitum reclinatum* Gray, $n = 8$, $2n = 16$; *A. uncinatum* L. $n = 8$, $2n = 16$; *Aquilegia baikalensis*? $2n = 14$; *A. coccinea* Small, $n = 7$; *A. dichroa* Freyn, $2n = 14$; *A. einseleana* Fr. Schultz, $2n = 14$; *A. glandulosa* Fisch., $2n = 14$; *A. hirsutissima*?, $2n = 28$; *A. jucunda* (*glandulosa*?), $2n = 14$; *A. longissima* Gray, $2n = 14$; *A. skinneri* Hook., $n = 7$, $2n = 14$; *Clematis addisonii* Britton, $n = 8$; *C. armandi* Franch., $2n = 16$; *C. brevicaudata* DC., $2n = 16$; *C. crispa* L., $2n = 16$; *C. dioica* L., $2n = 16$; *C. douglassii* Hook., $2n = 16$; *C. fremontii* Wats., $2n = 16$; *C. globosa* Royle (*orientalis* L.), $2n = 16$; *C. ochroleuca* Ait., $2n = 16$; *C. scottii* Porter, $2n = 16$; *Delphium bulleyanum* Forrest,

$2n = 32$; *D. carolinianum* Walt. (*azureum* Michx.), $2n = 32$; *D. caucasicum* C. A. Mey., $2n = 32$; *D. duhmbergii* Huth, $2n = 32$; *D. flexuosum* Rafin., $2n = 32$; *D. formosum* Boiss. & Huet, $2n = 32$; *D. gayanum* Willmott, $2n = 16$; *D. grandiflorum* L., $n = 8$; *D. penardi* Huth, $n = 8$; *D. peregrinum* L., $n = 8$; *D. pictum* Willd. (requienii DC.), $2n = 16$; *D. scopulorum* Gray, $n = 8$; *D. tricorne* Michx., $n = 8$; *D. yunnanense* Franch., $n = 8$; *Helleborus abschasicus* A. Br., $2n = 32$; *Ranunculus armeniacus* Boiss. & Huet (*anemonaefolius* DC.), $2n = 14$; *R. cassius* Boiss., $2n = 14$; *R. lomatocarpus* Fisch. & Mey., $2n = 32$; *Thalictrum coriaceum* (Britton) Small, $2n = 70$; *T. majus* Crantz, $2n = 28$; *T. revolutum* DC., $2n =$ ca. 133; *Trollius yunnanensis* Ulbr., $2n = 16$.

3. In all, the chromosomes of 109 species involving 19 genera have been studied. Camera-lucida drawings of all the species studied have been made to the same scale and arranged in twelve plates with 132 figures. (Magnification of plates changed at publication.) This is the largest single collection of chromosome drawings of the Ranunculaceae at present available.

4. The following basic chromosome numbers have been selected for the Ranunculaceae: 5, 7, 8, 9, and 13. The highest degree of polyploidy has been reached in the 7- and 8-series with the highest $2n$-numbers = 154 and 128 respectively.

5. A consideration of the effect of polyploidy in the evolution versus the speciation of the family has been discussed and the primarily diploid and the primarily polyploid genera of both the 7- and 8-series compared. An evaluation of the significance of polyploidy, and the relative roles of polyploidy versus other factors in evolution of the woody habit in the Ranunculaceae has been attempted.

6. A phyletic rearrangement of the genera and tribes of the family has been made on the basis of chromosome-type, size, and basic chromosome numbers of the family. On the same data a polyphyletic origin of the various tribes of the family from some ancestral group has been suggested and has been illustrated by phylogenetic charts comparing the classical, and the author's classifications.

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PLATE I

FIG. 1. *Aconitum uncinatum* $2n = 16$.
FIG. 2. *Aconitum reclinatum* $2n = 16$.
FIG. 3. *Aconitum uncinatum* M I $n = 8$.
FIG. 4. *Aconitum reclinatum* M I $n = 8$.
FIG. 5. *Aconitum Napellus* $2n = 32$.
FIG. 6. *Actaea alba* $2n = 16$.
FIG. 7. *Adonis aestivalis* $2n = 32$.
FIG. 8. *Adonis autumnalis* $2n = 32$.

Magnification ca. 2550 ×.

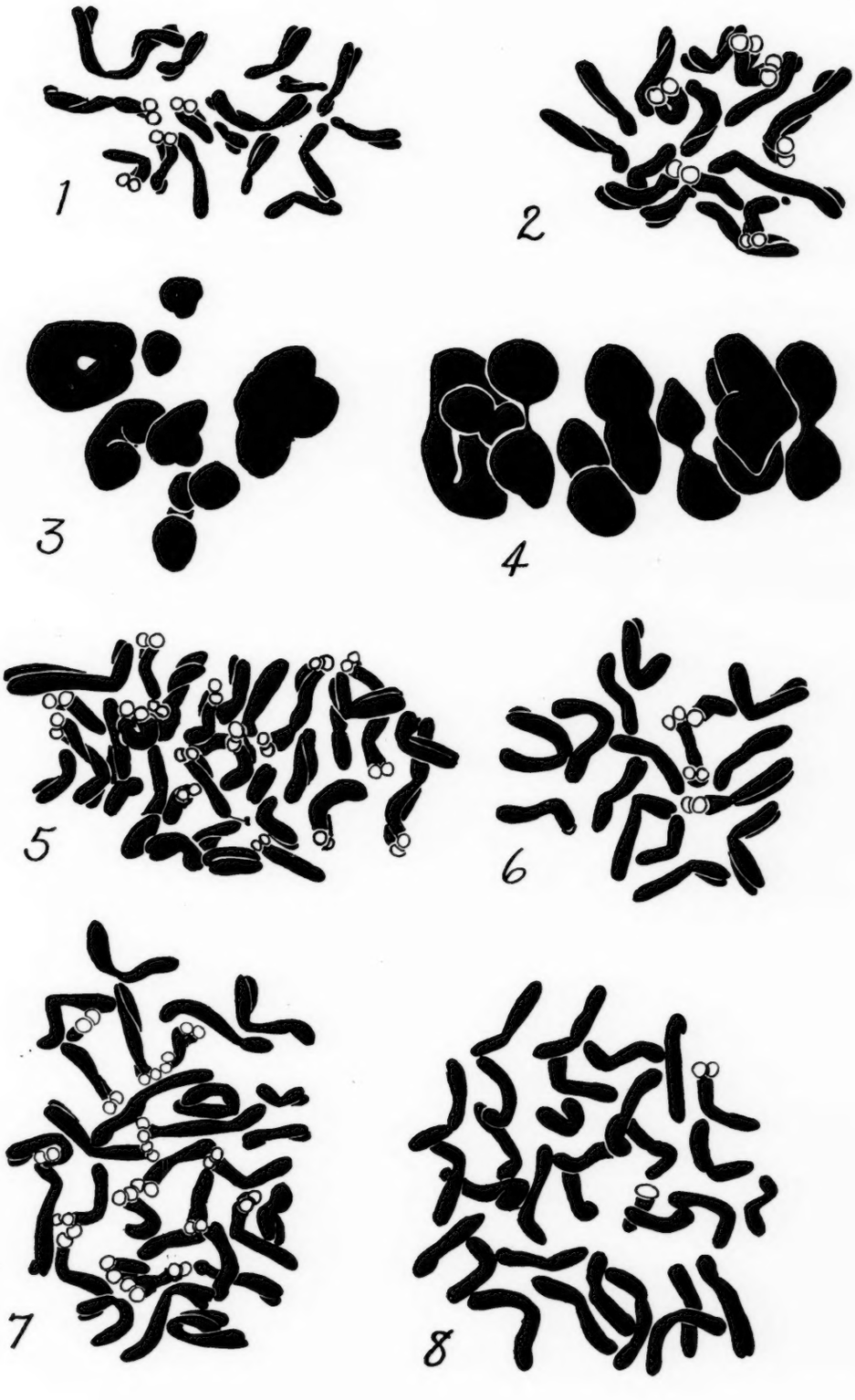
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PLATE II

FIG. 9. *Anemone cylindrica* M I $n = 8$.
FIG. 10. *Anemone sylvestris* $2n = 32$.
FIG. 11. *Anemone pulsatilla* $2n = 32$.
FIG. 12. *Anemone rivularis* $2n = 16$.
FIG. 13. *Anemone cylindrica* $2n = 16$.
FIG. 14. *Anemonella thalictroides* $2n = 14$.
FIG. 15. *Anemone rivularis* var. *barbulata* $2n = 16$.
FIG. 16. *Anemone virginiana* M I $n = 8$.
FIG. 17. *Anemone Leveillei* $2n = 16$.
FIG. 18. *Anemone japonica* M I $n = 8$.

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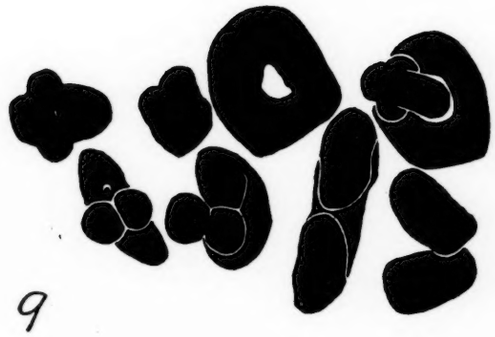

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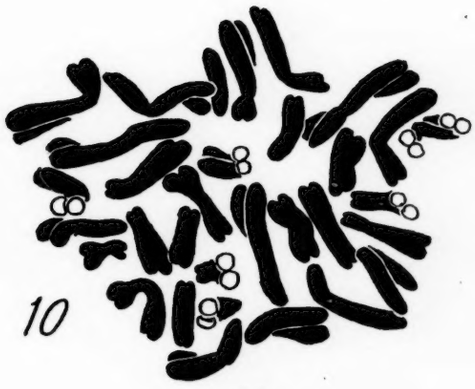

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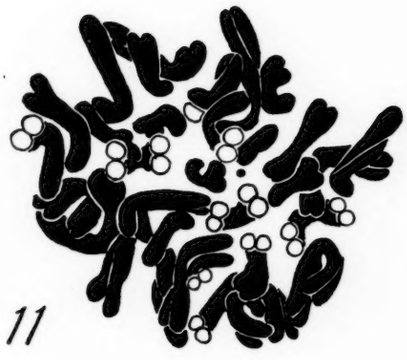

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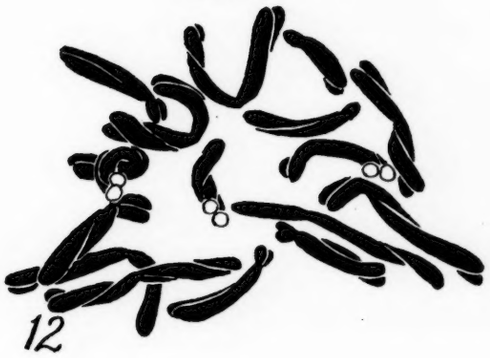

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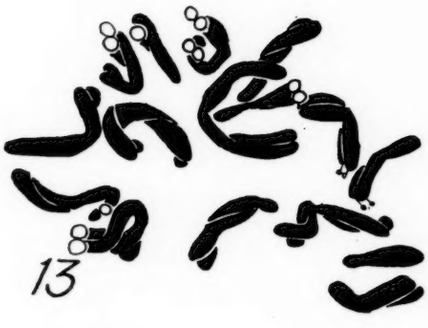

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PLATE III

FIG. 19. *Aquilegia baikalensis* $2n = 14$.
FIG. 20. *Aquilegia alpina* $2n = 14$.
FIG. 21. *Aquilegia canadensis* M I $n = 7$.
FIG. 22. *Aquilegia canadensis* M II $n = 7$.
FIG. 23. *Aquilegia canadensis* $2n = 14$.
FIG. 24. *Aquilegia chrysantha* $2n = 14$.
FIG. 25. *Aquilegia coccinea* M I $n = 7$.
FIG. 26. *Aquilegia dichroa* $2n = 14$.
FIG. 27. *Aquilegia einseleana* $2n = 14$.
FIG. 28. *Aquilegia glandulosa* $2n = 14$.
FIG. 29. *Aquilegia jucunda* $2n = 14$.
FIG. 30. *Aquilegia hirsutissima* $2n = 28$.
FIG. 31. *Aquilegia longissima* $2n = 14$.
FIG. 32. *Aquilegia longissima* M I $n = 7$.
FIG. 33. *Aquilegia longissima* M II $n = 7$.
FIG. 34. *Aquilegia skinneri* M I $n = 7$.
FIG. 35. *Aquilegia skinneri* M II $n = 7$.
FIG. 36. *Aquilegia skinneri* $2n = 14$.
FIG. 37. *Aquilegia vulgaris* M I $n = 7$.
FIG. 38. *Aquilegia vulgaris* M II $n = 7$.
FIG. 39. *Aquilegia vulgaris* $2n = 14$.

Magnification ca. 3100 ×.

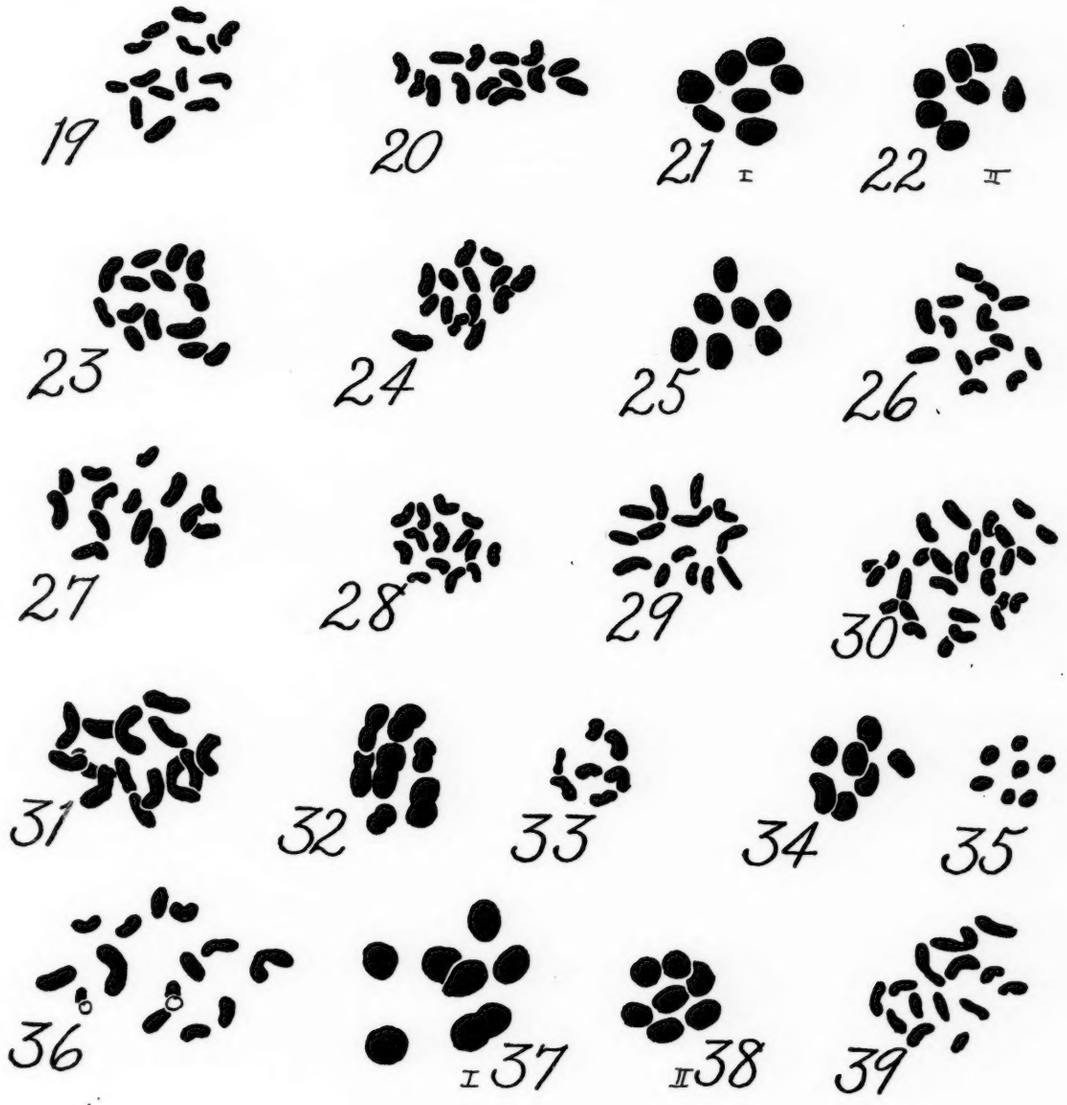
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PLATE IV

FIG. 40. *Clematis armandi* $2n = 16$.
FIG. 41. *Clematis brevicaudata* $2n = 16$.
FIG. 42. *Clematis crispa* $2n = 16$.
FIG. 43. *Clematis dioicus* $2n = 16$.
FIG. 44. *Clematis douglassii* $2n = 16$.
FIG. 45. *Clematis fremontii* $2n = 16$.
FIG. 46. *Clematis globosa* $2n = 16$.
FIG. 47. *Clematis heraclaeafolia* $2n = 16$.
FIG. 48. *Clematis ligusticifolia* $2n = 16$.
FIG. 49. *Clematis Ville de Lyon* $2n = 16$.
FIG. 50. *Clematis integrifolia* $2n = 16$.
FIG. 51. *Clematis ochroleuca* $2n = 16$.

Magnification ca. 2550 ×.

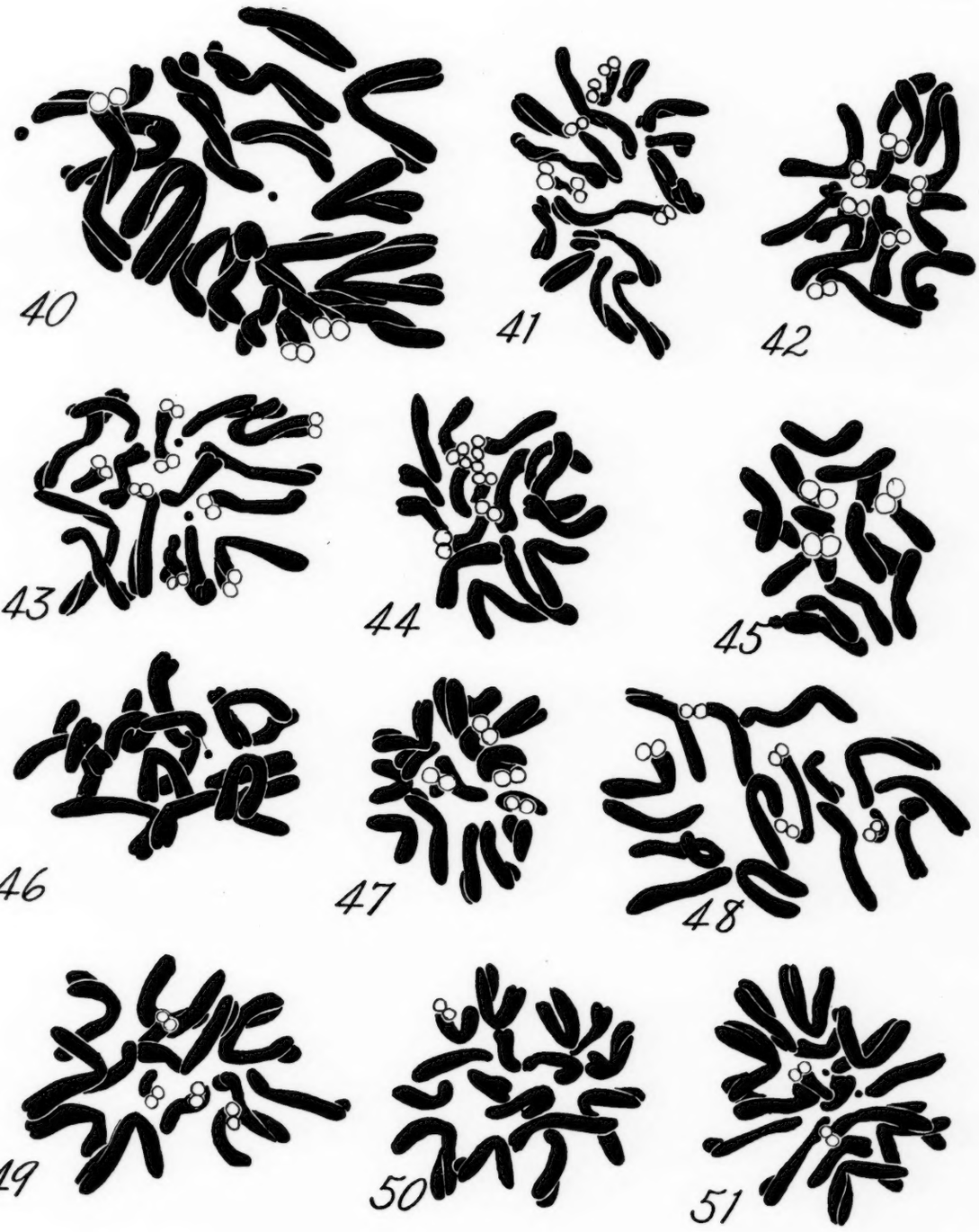
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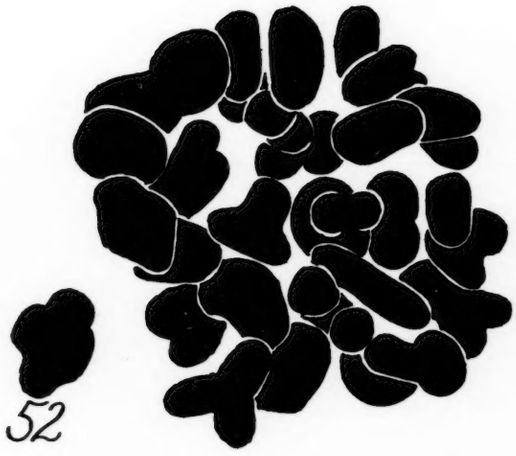
PLATE V

FIG. 52. *Clematis paniculata* M I $n = 32$ (showing ca. 30).
FIG. 53. *Clematis virginiana* M I $n = 8$.
FIG. 54. *Clematis addisonii* M I $n = 8$.
FIG. 55. *Clematis scottii* $2n = 16$.
FIG. 56. *Clematis Baron Veillard* $2n = 16$.
FIG. 57. *Clematis tangutica* $2n = 16$.
FIG. 58. *Clematis tangutica* M I $n = 8$.
FIG. 59. *Clematis heraclaeafolia* var. *davidiana* M I $n = 8$.
FIG. 60. *Clematis texensis* $2n = 16$.
FIG. 61. *Caltha palustris* $2n = 32$.
FIG. 62. *Clematis paniculata* $2n = 16$.

Magnification ca. 2550 ×.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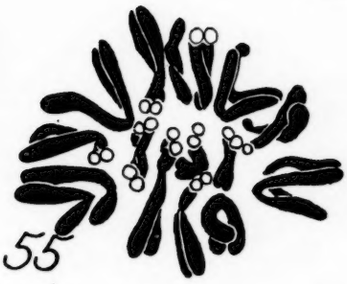
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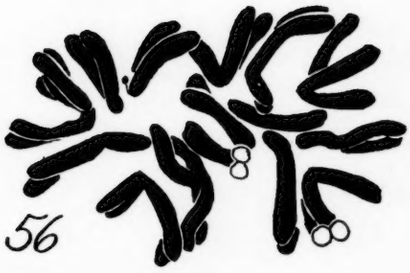
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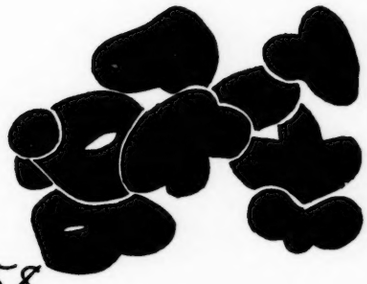
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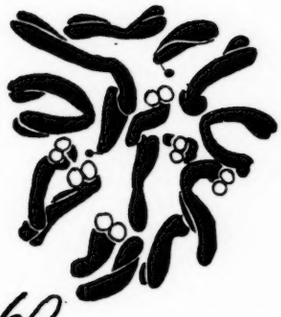
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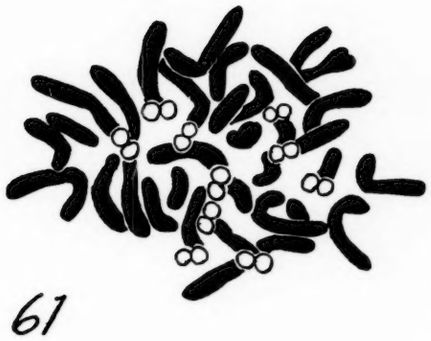
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PLATE VI

FIG. 63. *Cimicifuga racemosa* M I $n = 8$.
FIG. 64. *Cimicifuga racemosa* M II $n = 8$.
FIG. 65. *Cimicifuga racemosa* $2n = 16$.
FIG. 66. *Delphinium grandiflorum* M I $n = 8$.
FIG. 67. *Delphinium ajacis* $2n = 16$.
FIG. 68. *Delphinium bulleyanum* $2n = 32$.
FIG. 69. *Delphinium carolinianum* $2n = 32$.
FIG. 70. *Delphinium duhmbergii* $2n = 32$.
FIG. 71. *Delphinium pictum* (*requienii*) $2n = 16$.
FIG. 72. *Delphinium caucasicum* $2n = 32$.
FIG. 73. *Delphinium elatum* $2n = 32$.
FIG. 74. *Delphinium flexuosum* $2n = 32$.
FIG. 75. *Delphinium consolida* $2n = 16$.

Magnification ca. 2550 ×.

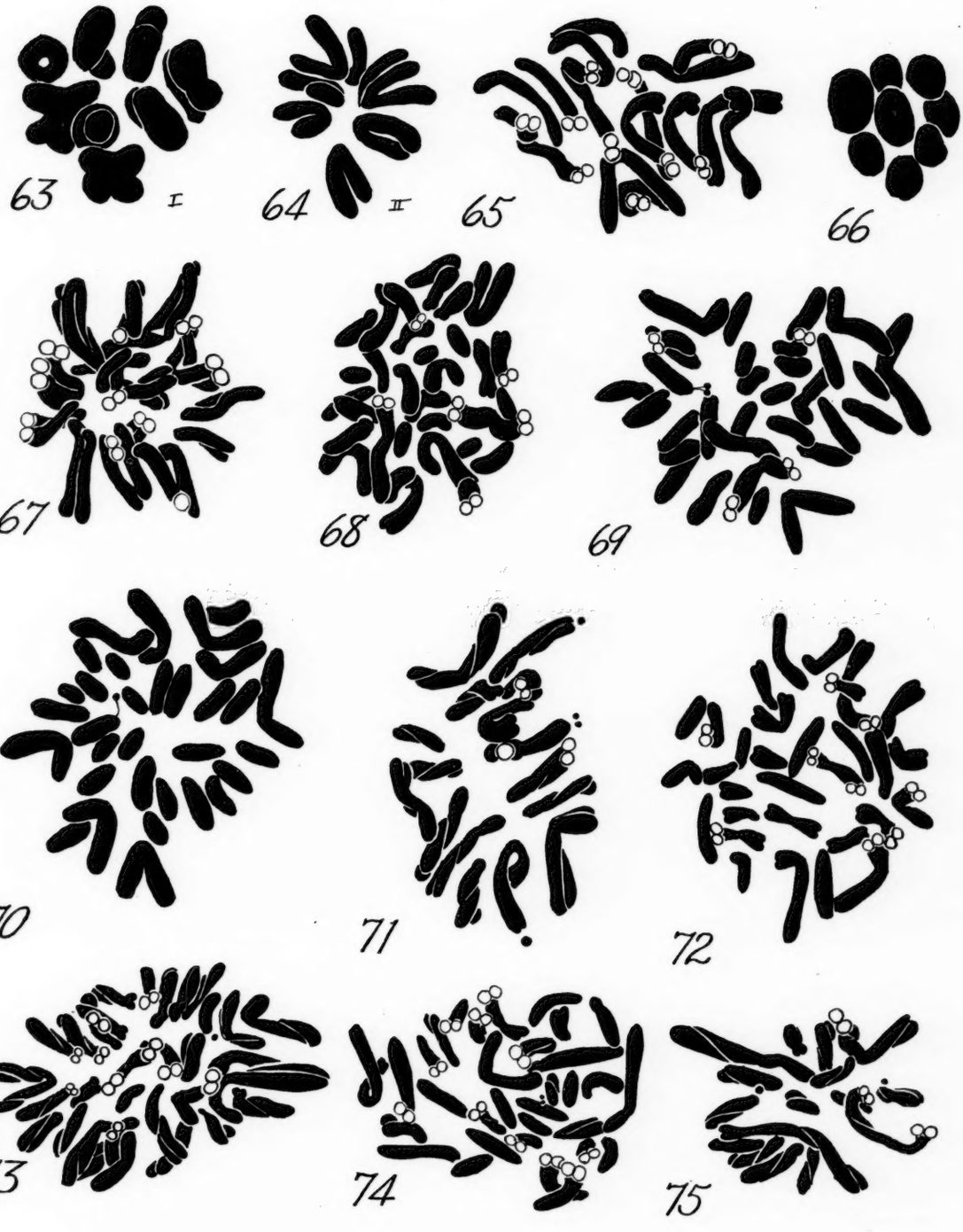
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PLATE VII

FIG. 76. *Delphinium orientale* $2n = 16$.
FIG. 77. *Delphinium scopulorum* M I $n = 8$.
FIG. 78. *Delphinium consolida* M I $n = 8$.
FIG. 79. *Delphinium peregrinum* M I $n = 8$.
FIG. 80. *Delphinium penardi* M I $n = 8$.
FIG. 81. *Delphinium yunnanense* M I $n = 8$.
FIG. 82. *Delphinium gayanum* $2n = 16$.
FIG. 83. *Delphinium tricorne* M I $n = 8$.
FIG. 84. *Delphinium scopulorum* $2n = 16$.
FIG. 85. *Delphinium formosum* $2n = 32$.
FIG. 86. *Delphinium yunnanense* $2n = 32$ (from tetrpl. root) see Fig. 81.
FIG. 87. *Delphinium grandiflorum* $2n = 32$ (from tetrpl. root) see Fig. 66.

Magnification ca. 2550 ×.

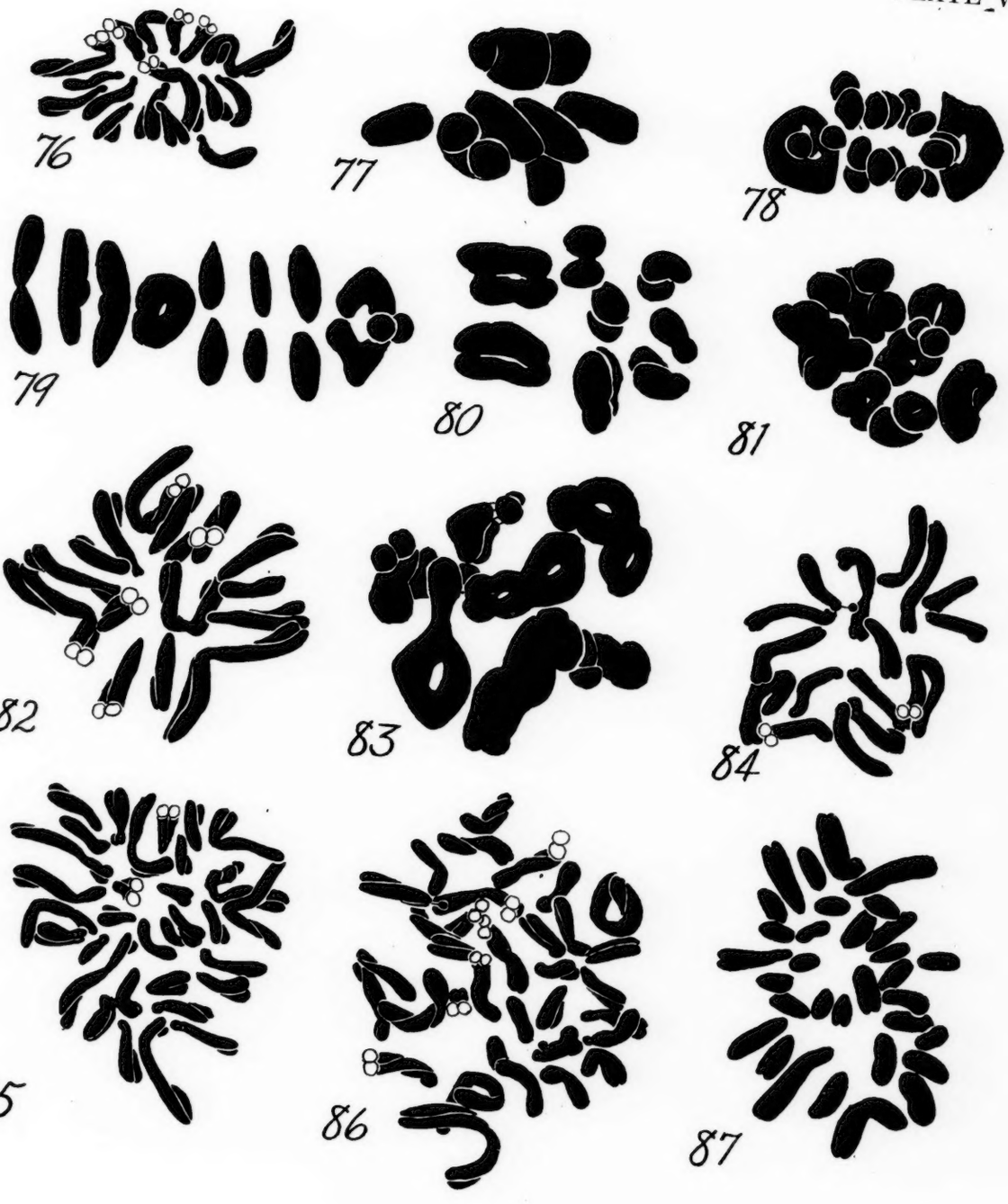
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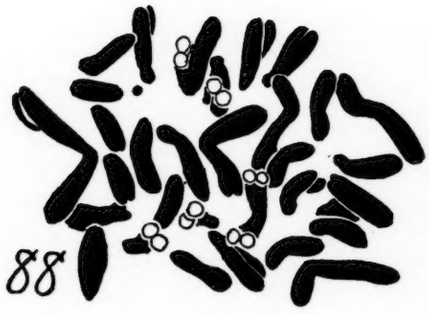
PLATE VIII

FIG. 88. *Delphinium* (Wrexham hybrids) $2n = 32$.
FIG. 89. *Isopyrum fumarioides* $2n = 14$.
FIG. 90. *Eranthis hiemalis* $2n = 48$ (from hexapl. root).
FIG. 91. *Helleborus abschasicus* $2n = 32$.
FIG. 92. *Helleborus foetidus* $2n = 32$.
FIG. 93. *Hepatica triloba* $2n = 14$.
FIG. 94. *Nigella* (Miss Jekyll) $2n = 12$.

Magnification ca. 3100 ×.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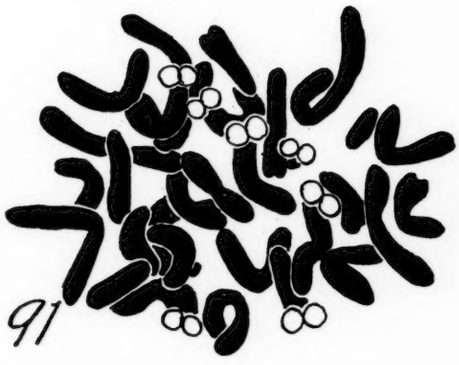
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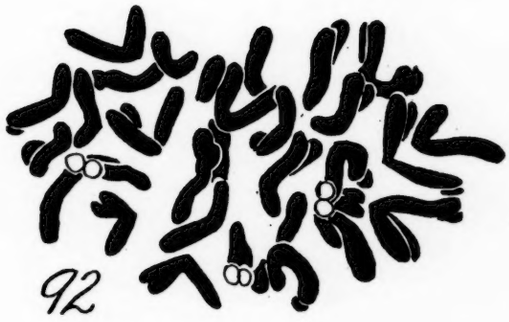
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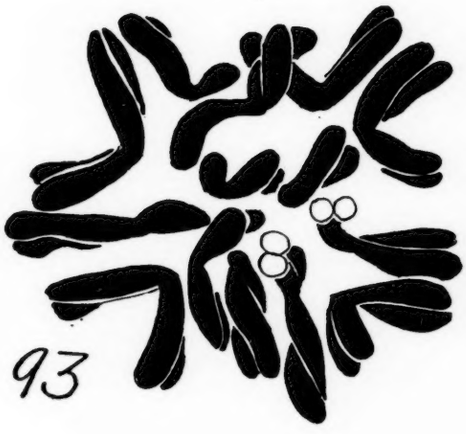
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PLATE IX

FIG. 95. *Nigella arvensis* M I $n = 6$.
FIG. 96. *Nigella arvensis* $2n = 12$.
FIG. 97. *Nigella damascena* M I $n = 6$.
FIG. 98. *Nigella sativa* M I $n = 6$.
FIG. 99. *Nigella damascena* $2n = 12$.
FIG. 100. *Nigella nigellastrum* (*garidella*) M I $n = 6$.
FIG. 101. *Nigella sativa* $2n = 12$.
FIG. 102. *Nigella orientalis* M I $n = 6$.
FIG. 103. *Nigella orientalis* $2n = 12$.
FIG. 104. *Nigella hispanica* M I $n = 6$.
FIG. 105. *Nigella hispanica* $2n = 12$.

Magnification ca. 2300 ×.

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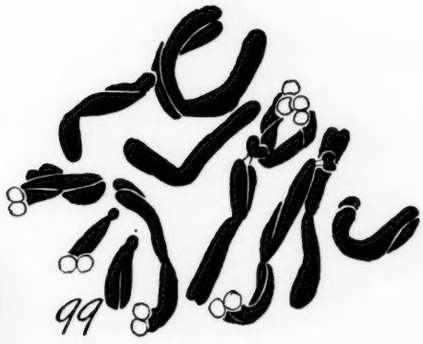
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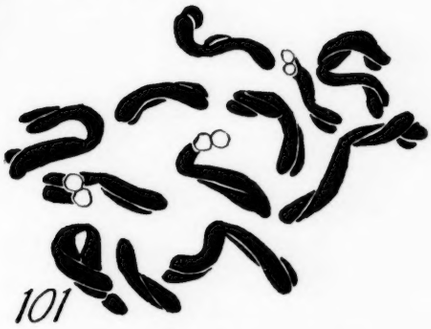
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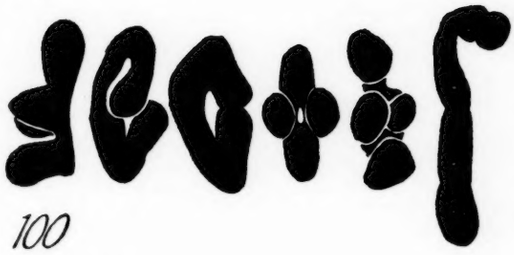
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PLATE X

FIG. 106. *Paeonia brownii* $2n = 10$.
FIG. 107. *Paeonia veitchii* $2n = 10$.
FIG. 108. *Paeonia officinalis* $2n = 20$.

Magnification ca. 3100 ×.

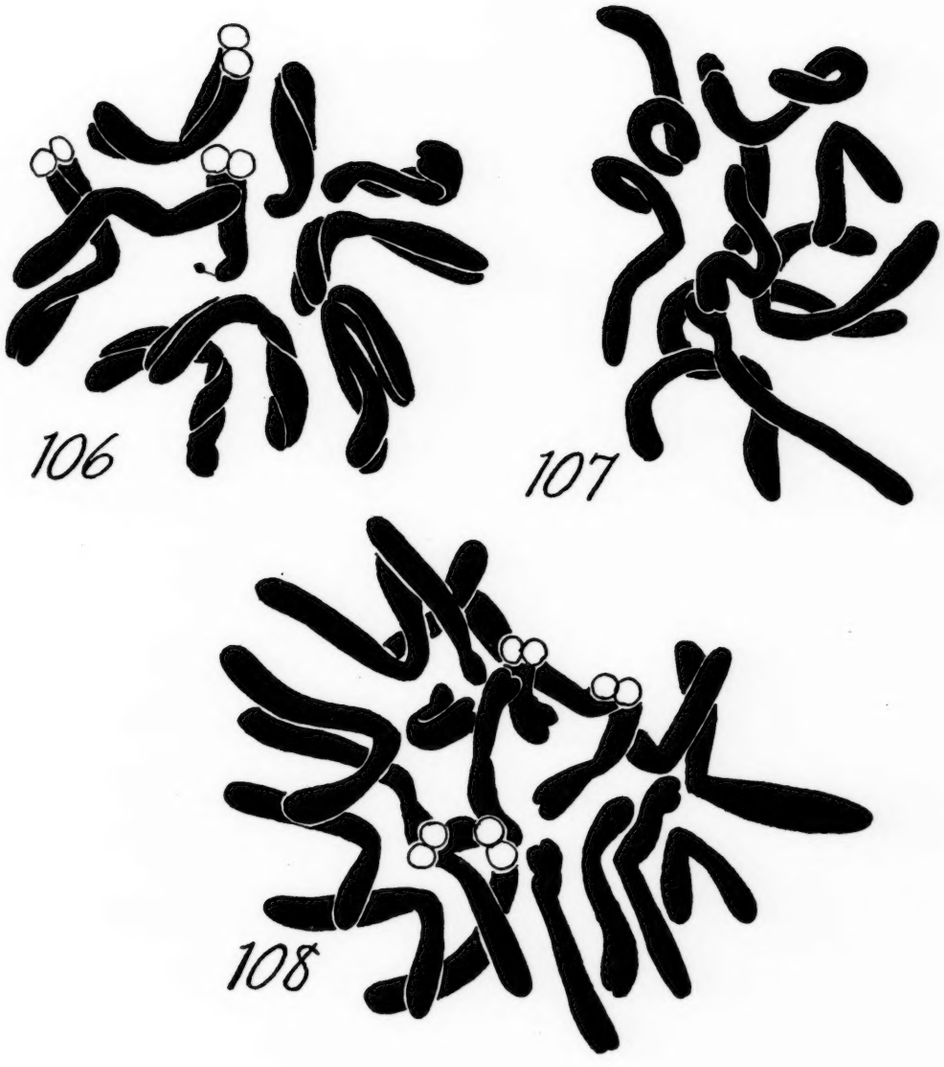
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PLATE XI

FIG. 109. *Ranunculus armeniacus* $2n = 14$.
FIG. 110. *Ranunculus acris* $2n = 14$.
FIG. 111. *Ranunculus aconitifolius* $2n = 14$.
FIG. 112. *Ranunculus cassius* $2n = 14$.
FIG. 113. *Ranunculus auricomus* $2n = 32$.
FIG. 114. *Ranunculus flammula* $2n = 32$.
FIG. 115. *Ranunculus chius* $2n = 16$.
FIG. 116. *Ranunculus lomatocarpus* $2n = 32$.
FIG. 117. *Ranunculus trilobus* $2n = 48$.
FIG. 118. *Ranunculus septentrionalis* $2n = 64$.
FIG. 119. *Ranunculus muricatus* $2n = 48$.
FIG. 120. *Ranunculus nemorosus* var. *polyanthemoides* $2n = 16$.
FIG. 121. *Ranunculus sceleratus* $2n = 32$.
FIG. 122. *Ranunculus nelsoni* M II $n = 8$.
FIG. 123. *Ranunculus nelsoni* M I $n = 8$.

Magnification ca. 2550 ×.

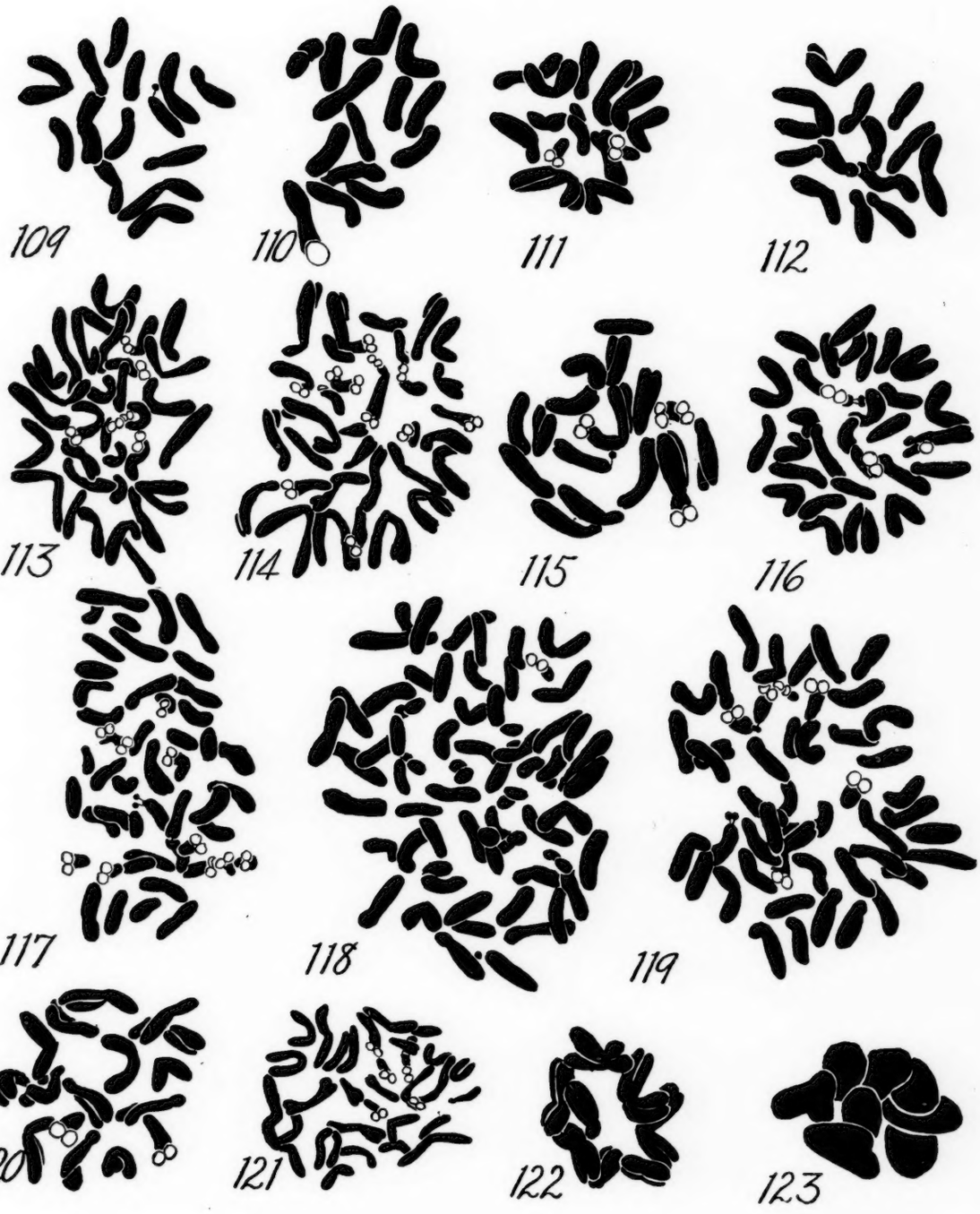
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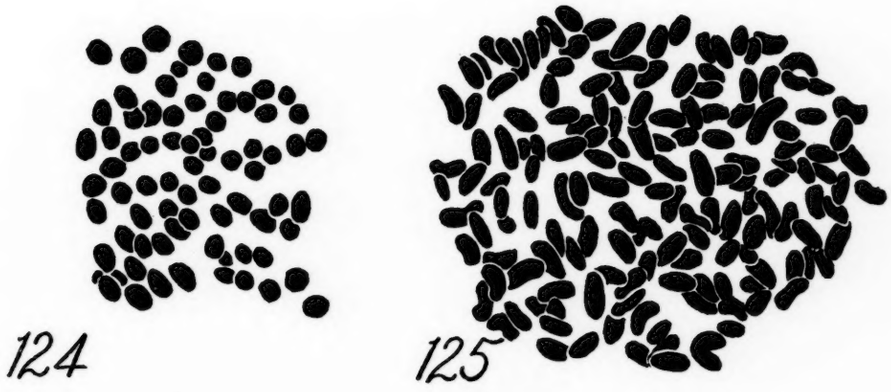
PLATE XII

FIG. 124. *Thalictrum polygamum* M I $n = 74$ (77, see Fig. 125).
FIG. 125. *Thalictrum polygamum* $2n = 154$.
FIG. 126. *Thalictrum minus* M I $n = 21$.
FIG. 127. *Thalictrum coriaceum* $2n = 70$.
FIG. 128. *Thalictrum majus* $2n = 28$.
FIG. 129. *Thalictrum minus* $2n = 42$.
FIG. 130. *Thalictrum flavum* subsp. *glaucum* $2n = 28$.
FIG. 131. *Thalictrum revolutum* $2n =$ ca. 133.
FIG. 132. *Trollius yunnanensis* $2n = 16$.

Magnification ca. 3100 ×.



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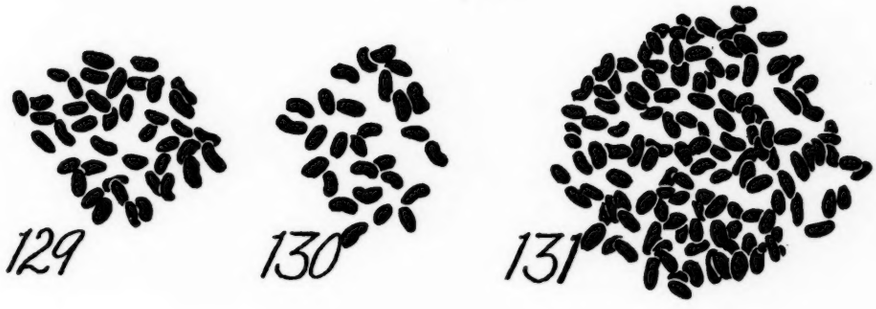

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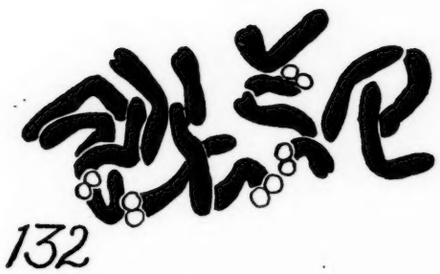

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